The Immature Stages of the Subfamily Phlebotominae in Panama (Diptera: Psychodidae)

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INTRODUCTION

Species of the genus Phlebotomus, commonly known as sand flies, are distributed chiefly in the moist tropical regions of the world, but a number of them range into semi-arid areas. The genus probably reaches its peak in diversification in the American tropics, where over 200 species have been described. The Phlebotominae represent one of several groups within the order Diptera which have acquired independently the development of the bloodsucking habit. Were it not for this habit, this subfamily would indeed be an obscure part of the insect fauna, for the adults secrete themselves in dark crevices, animal burrows, caves, etc., during the day and emerge only after dark, flying silently and seldom far from their breeding places. Even more secretive and unobservable are the immature stages. Oviposition, larval development and pupation apparently take place in or near the soil, and these forms are seldom discovered. Because of this, our knowledge of them has increased very little since the immature stages were first observed and described nearly sixty years ago.

The purpose of the present study is to fill in many of the gaps in our knowledge of the immature stages of the species encountered in Panama. Long known as disease vectors in other regions, Phlebotomus in Panama have recently been the object of concern because of the widespread occurrence of leishmaniasis in the country. The staff of the Gorgas Memorial Laboratory in Panama has recently been investigating the whole problem of leishmaniasis transmission, and it was as a part of this research team that I carried out the field ecological studies herein described.

One of the greatest needs is a comparative taxonomic study of the larval stage, which is necessary before larvae can be reliably determined. Although several descriptions of larvae have been published, there is no standard use of characters at present, with the result that many of the species illustrated and described cannot be identified. It is hoped that this study will help to standardize the use of characters for species identification. The mature larva (fourth instar) is emphasized, partly because of the availability of specimens and partly because the characters are more easily seen and studied. The egg stage is not included at this time, and some of the early instars of several species are not known. The early instars which are available are only briefly treated and are compared with the fourth instar. The pupa is described only in general.

The development of the immature stages, as observed in laboratory cultures, has been thoroughly described by Johnson and Hertig (1961) and thus is not repeated here.

ECOLOGICAL STUDIES

Distribution of Phlebotomus in Panama

Nearly all of Panama has a tropical climate; only in the high mountainous region, above 8,500 feet, in the western end of the country is the climate temperate. The Atlantic slope and the Pacific side of eastern Darien Province receive up to 150 inches of rainfall annually, mostly in the wet season from about May to December, but enough falls during the remaining months to insure a continually evergreen forest. On the Pacific slope, especially in the western part of the country and including approximately the southern half of the Canal Zone, the annual rainfall is about 85 inches, nearly all of it in the wet season. During the dry season, much of the vegetation turns brown and loses its leaves, the smaller watercourses dry up, and the soil becomes hard and cracked. Much of this area is open grassland or savanna. On the higher ridges and slopes of the mountains above 3,000 feet elevation, there is more precipitation due to condensation from the northeast trade winds. These elevations are almost continuously enveloped in clouds and the vegetation is nearly always dripping with moisture. The trees are characteristically somewhat dwarfed, and epiphytes, such as mosses, bromeliads and orchids are extremely abundant. Nearly all of the field studies in this work were carried out in the vicinity of the Canal Zone, from Cerro Campana on the west, to Cerro Azul, near the head-waters of the Pecora River, on the east, and on both the Pacific and Atlantic sides of the Isthmus.

All but a few of the species of Phlebotomus occurring in Panama have been collected in this area. However, they are not evenly distributed

throughout their range. Several species are absent from extensive areas, especially where man has disturbed the natural vegetation. This is most noticeable where tall grass has replaced the original forest which was removed for cultivation. In such areas at most one or two species of Phlebotomus may be found, in contrast to the undisturbed forest of the Atlantic slope, where the great majority of the species have been collected. Certain species seem to be limited to habitats which apparently are not suitable for others. For example, P. atroclavatus Knab, P. cayennensis Floch and Abonnenc, and P. chiapanensis Dampf are never collected far from the ocean shore and are often found in crevices of old ruins. Other species are rarely taken there. P. hartmanni Fairchild and Hertig is apparently limited to the higher and cooler forest near the cloud zone, where few other species are encountered. Perhaps the most ubiquitous species are P. trinidadensis Newstead and P. vespertilionis Fairchild and Hertig, which may be found in a wide variety of habitats, sometimes in great abundance.

Breeding Places

Historical review

Perhaps the first Phlebotomus larvae ever taken from natural habitats and recognized as such were those found by an assistant of Grassi in a cellar in Rome and reported in 1907. Several adults were reared from these larvae and described by Grassi as a new species, P. mascittii.

Early investigations by Marett (1910, 1913, 1915), Newstead (1911) and Whittingham and Rook (1923) in Malta, Howlett (1913) and Mitter (1919) in India, and King (1913, 1914) in the Sudan turned up only a few larvae

and pupae from natural habitats. Many searches by these workers and others proved fruitless, and the location of breeding places was often merely assumed because of the proximity of resting adults.

It was not until the work of McCombie-Young, Richmond and Brendish (1926) in India that substantial numbers of larvae and pupae were found. These workers were the first to apply the flotation technique in the search for Phlebotomus, and by this process, in which a saturated solution of sugar was used, they recovered immature stages of P. papatasi from soil samples taken in the vicinity of human or animal habitations.

Shortt, Smith and Swaminath (1930, 1932) also used this method in finding the breeding places of P. argentipes in Assam. They found numerous larvae of this species in the top five inches of soil rich in organic matter, in and around houses. Smith, Mukerjee and Lal (1936), while studying the breeding places of P. argentipes, found the larvae most abundant in loose soil within 20 yards of human or animal dwellings. They also used the flotation technique and recovered, besides P. argentipes, immature stages of P. papatasi, P. shortii Adler and Theodor, P. squamipleuris Newstead and P. babu Ann., which were then reared to the adult stage.

In other areas, Jerace (1939) in Italy found larvae in debris and soil cracks at or near the base of old walls. Wanson (1942) in the Belgian Congo found pupae of P. freetownensis Sinton, P. schwetzi Adler, Theodor and Parrot, P. squamipleuris, P. freetownensis niger Parrot and Schwetz, and P. wansoni Parrot in soil near latrines. Najera (1946) in Spain found larvae in 14 of 130 samples of rubbish taken along streets in Madrid.

In Turkmenistan, Petrishcheva and others (1932, 1935, 1949a, 1949b, 1949c) investigated many possible habitats and obtained immature stages

from the following places: land tortoise nest, mammal burrows, dry excreta of small domestic animals, dead leaves and rubbish, gerbil nests and bird nests from holes in soil banks. Soil samples from these habitats were processed by flotation in a saturated solution of NaCl. In addition, they obtained many adults by placing cages over the entrances of burrows and tree holes and over the ground.

During the course of studies of breeding places by Petrischeva and Izyumskaya (1941) in Sebastopol, six tons of soil were processed, comprising 965 samples, of which 28 contained a total of 61 larvae and 91 pupae. More than 50 per cent of the larvae and pupae were taken from floors of houses and animal shelters, 32 per cent from cracks in soil and from burrows of rodents and 18 per cent from under stones at the base of walls. None was found in dung heaps, debris under trees, litter from animal shelters nor in rich soil from gardens.

Nothing was known of the breeding places of New World species until Ferreira, Deane and Mangabeira (1938) in Brazil reported finding four larvae in material at the base of a tree. Also in Brazil, Lutz (in Castro, 1939) obtained adults in cages placed over soil of the forest floor, and Coutinho and Barretto (1941) found one larva of P. fischeri Pinto in soil taken at the base of a tree, from which soil an adult of this species also emerged.

Elsewhere, Pifano (1941) in Venezuela found about a dozen larvae in a hole in a wall of a house. Hertig (1942) in Peru examined material from a rock wall which was suspected to be a breeding place because of the presence of white, newly emerged adults. One pupal case was found.

In more recent years, Forattini (1954) in Brazil reared twelve adults of P. intermedius Lutz and Neiva from soil samples taken from a

pigpen, and one of the same species from soil at the base of a bush and one of P. pessoai Coutinho and Barretto from soil at the edge of a stream, both in forested areas. Deane and Deane (1957), also in Brazil, obtained 32 specimens from 241 soil samples, most of which they either processed by flotation in salt solution or kept in the laboratory for emergence of adults. Three species were identified: P. cortelezzii Brethes, P. longipalpis Lutz and Neiva and P. oswaldoi Mang. The positive samples were taken from the ground in a mule shelter, under rocks, in rock crevices, from the floors of caves, and in scrapings from the trunks of two trees.

Despite the great amount of time and careful work involved, the above investigations in the New World thus turned up little more than sixty specimens, remarkably few considering the effort expended and the abundance of the adults.

Present study

From September 1957 to July 1960 an intensive search was carried out for the breeding places of Phlebotomus in Panama, with especial interest in the six common man-biting species of this area--P. trapidoi F. and H., P. sanguinarius F. and H., P. gomezi Nitz., P. panamensis Shan., P. ylephiletor F. and H., P. pessoana Barr. Preliminary processing of soil samples by Drs. Marshal Hertig and Phyllis T. Johnson of the Gorgas Memorial Laboratory, beginning in May 1957, had turned up larvae of Phlebotomus for the first time in Panama. Since then 370 soil samples were processed, in addition to the numerous direct examinations in the field, yielding 2258 larvae and pupae, 600 of which have been reared to the adult stage and determined. Samples were taken each month of the year but mostly during the rainy and early dry seasons. Several

localities on both sides of the Isthmus, in or near the Canal Zone, from sea level to about 2000 feet elevation, were repeatedly visited for obtaining soil samples and searching for immature stages. The places most intensively investigated were: Cerro Galera, on the Pacific side of the Canal Zone; Piña Area, on the Atlantic side near the mouth of the Chagres River; Madden Forest Preserve, nearly midway across the Isthmus in the Canal Zone; and Cerro Campana, in the Republic of Panama about 50 kilometers west of the Canal Zone. Several other areas in the Canal Zone were visited, particularly along abandoned army roads, where the forest is relatively undisturbed.

Methods

The scantiness of information on breeding places of Phlebotomus is no doubt largely due to the difficulty of isolating the immature stages from the soil. Four methods have previously been used by other workers in finding breeding places: (1) careful direct examination of the soil, debris, etc., (2) placing emergence cages over suspected plots of ground, (3) keeping soil samples in the laboratory within containers and making daily observations for emerging adults, and (4) processing soil by flotation or screening or both. All of these methods require considerable time and patience, but it was found that a combination of flotation using a saturated sugar solution and washing through screens is very satisfactory for ordinary soil samples. It has advantages over methods which involve awaiting the emergence of adults either in the field or laboratory, in that the larvae and pupae in a given sample are recovered at once. Furthermore, the process itself does not harm the larvae or pupae, which can then be reared to the adult stage and identified.

Direct examination is satisfactory for dead leaves and other large objects, but it is very tedious and time-consuming if the sample consists of soil or debris.

The screening-flotation method used in this study is designed to isolate the larvae with as little extraneous material as possible. The samples being processed consist of material which falls into three density categories: heavier soil particles which sink and offer no problem; live insects and other members of the soil fauna which sink in water but float in a denser liquid such as saturated sugar solution; material lighter than water; such as bits of leaf, wood and bark, which is present in considerable quantity and complicates the search for larvae. The treatment of the screened fractions with water alone gets rid of this water-floatable material.

The details of the method in practice are as follows: For samples consisting mostly of soil and which do not contain many leaves, twigs or other large objects, (1) the soil is placed in a pan with enough saturated sugar solution added to cover it to a depth of about two inches. After considerable agitation by stirring with a tube through which air is bubbled, the sample is let stand for several minutes. (2) The sugar solution with floating material is then decanted through closely woven Nylon cloth, from which the collected material is washed into a series of three nested, brass gauze sieves, eight inches in diameter, with 20 40 and 60 meshes per inch. With samples containing many leaves or other large floatable objects, the preliminary flotation is omitted, and the sample is washed with running water directly into the screens. (3) Most of the larvae are retained by the 40 and 60 mesh screens. These fractions are washed separately into 500 ml. cylinders,

which are then filled with water. After allowing a few minutes for any larvae to settle, the water is poured off, thus eliminating the bits of wood, leaves and other water-floatable material. (4) The cylinders are then filled with sugar solution and left for about ten minutes to allow the living organisms to rise to the surface and the heavier particles to sink. (5) The sugar solution is decanted from the cylinder through a Nylon cloth strainer, which, together with the collected sugar-floatable material, is then transferred to a petri dish for examination under the microscope. Enough clean sugar solution is added to the petri dish to allow the living organisms to float. The cloth strainer, a little larger than the petri dish, is crimped radially with four staples so that it lies saucer-like in the petri dish. This is important for rapid microscopic examination, as the gently sloping cloth prevents excessive accumulation of particles around the edge of the surface of the liquid.

The entire washing-flotation process requires at least half an hour, or longer if much organic material is present. Sugar (sucrose) is used instead of salt or other chemicals because it is not toxic to Phlebotomus larvae. Most of the larvae are collected on the 40-mesh sieve, the first instar larvae usually passing onto the 60-mesh sieve. No real attempt has been made to recover the eggs. They readily pass through the 60-mesh sieve, and only two have been recovered.

Larval habitats

Table 1 lists the potential breeding places investigated for immature stages and the number of larvae or pupae recovered.

Table 2 lists by species and habitats those immature forms which were successfully reared to the adult stage and identified.

Table 1. Immature stages of *Phlebotomus* recovered from potential breeding places

Habitat	Screening-Flotation			Direct Examination
	No. of samples processed	No. of samples positive	No. of larvae or pupae recovered	Larvae or pupae recovered
Soil between buttressed roots	245	50	2,123	
Dead leaves from forest floor, not sheltered	55	19	39	37
Animal burrow	27	8	26	
Hollow tree	12	2	2	
Soil under overhanging roots	9	5	16	
Soil at base of tree, not sheltered	7	3	12	
Ant nest refuse	3	1	1	
Debris from tree hole	3	0	0	
Bark of living trees	2	0	0	
Soil under log	2	0	0	
Soil under rocks	3	0	0	1 pupal case
Soil refuse from chicken coop floor	1	0	0	
Cracks in soil	1	0	0	1 pupal case
TOTAL	370	88	2,219	39

Table 2. Immature stages of Phlebotomus from natural breeding places, reared to the adult stage and identified; listed by species and habitat

Species	Soil between buttressed roots	Soil from burrows	Soil under overhanging roots	Soil at base of tree	Dead leaves, forest floor
panamensis					8
pessoana					4
trapidoi	1	1			10
ylephiletor					2
camposi		1			
dysponetus	23		1		
galindoi	11			3	1
hamatus	427	5	5		
nordestinus	6				
ovallesi	24				
rubidulus	1				
serranus	35	1			
trinidadensis	13				
vespertilionis	1				
hansoni	16				
TOTAL	558	8	6	3	25

Buttressed roots. Most of the soil samples, each consisting of about one pint to one quart of soil, were taken from sheltered areas between buttressed roots, which are outgrowths at the bases of several species of tropical trees. These buttresses may be small and inconspicuous or so large that the space between them equals that of a small room. They often form narrow, deep crevices, or provide a wide variety of other situations, in most cases giving a certain amount of protection from sunlight, rain and wind. Associated with buttressed roots are communities of animals similar to those found in hollow trees and rock crevices. Certain species of snails, spiders, scorpions and other arachnoids, crickets, moths, crane flies, mosquitoes, as well as adult Phlebotomus, are typical inhabitants, at least during the day. The intensive collecting of adult sandflies by Drs. Fairchild and Hertig since 1943 has shown such cavities between buttressed roots to be the richest in species of Phlebotomus of all habitats investigated. At least 47 species have been taken there, but the bulk of the specimens were P. trinidadensis Newst. and P. ylephiletor F. and H., with smaller numbers of P. shannoni Dyar. The soil between buttressed roots often contains considerable organic matter, such as dead leaves, insect fragments and lizard feces, and would seem to be an ideal habitat for the immature stages of Phlebotomus. Therefore, particular attention was devoted to this habitat in the search for breeding places.

A total of 2,123 larvae and pupae, representing at least eleven species were recovered from this habitat. Most were in the top two inches of soil, with a few as deep as four inches. On two occasions, soil samples from the top inch of soil each yielded more than 200 larvae.

The results show little correlation between the numbers of larvae and adults of any given species found between buttressed roots. Only thirteen P. trinidadensis larvae have been recovered there, whereas adults of that species sometimes occur between buttressed roots by the hundreds. It may be that this species burrows to greater depts than those sampled, as it shows a burrowing tendency in laboratory cultures. However, half the larvae recovered were in the top inch of soil. The immature stages of P. shannoni, another common buttress inhabitant in the adult stage, have not been recovered; this species shows a surface-feeding tendency in laboratory cultures. P. hamatus F. and H., of which only five adults had been taken in years of collecting, overwhelmingly dominated the larval population of this habitat. Of the 558 buttress larvae reared and identified, 427 (76.5 per cent) were P. hamatus. In certain areas, during the rainy season, larvae of this species were present in more than half the samples taken. This species shows burrowing habits in laboratory culture, but it also was found chiefly in the top two-inch layer. Of the common man-biting species, only one larva of P. trapidoi or P. ylephiletor, did not survive to yield adults. Both of these species are surface-feeders in laboratory cultures.

Animal burrows. The 27 samples from animal burrows were taken from one to three feet inside the entrance; 26 larvae representing at least four species were recovered. One larva of P. trapidoi, the only man-biting species taken, was recovered from loose soil and leaf fragments scraped from the floor of a burrow. Again, P. hamatus was the dominant species, and of the species of which adults regularly inhabit burrows one larva of P. camposi Rodr. was found. It should be noted

that the immature stages of P. triramulus F. and H., which as adults often occurs in burrows in great numbers, have never been recovered from this or other habitats.

Hollow trees. Detritus at the bottom of hollow trees has yielded but two larvae, even though adults (vespertilionis group) are almost invariably resting inside the hollows. These larvae did not survive to the adult stage, but one is either P. vespertilionis or P. isovespertilionis. The inner surfaces of hollow trees have also been investigated, with negative results.

Rock crevices. While collecting adult Phlebotomus from spaces between large rocks, I found one pupal case attached to the underside of one of the rocks, about a foot from the opening. No other pupae or larvae have since been found in this habitat despite much searching. As the pupal case was not far above the ground surface, it is probable that the larva merely crawled up from the soil to pupate.

Forest floor; dead leaves. In rearing Phlebotomus in the laboratory, it was noted by Dr. P. T. Johnson that while some species burrowed in the food material, others always remained on top. She therefore thought it likely that these latter species would be found in nature on some surface, such as on decaying leaves and litter on the ground. This ultimately proved to be true for the several species concerned. Through the cooperation of Major R. A. Altman, MSC, U. S. Army, an area within Fort Kobbe Military Reservation was made available, where large numbers of P. panamensis had often appeared in a horse-baited mosquito trap during the rainy season. Several larvae of P. panamensis were obtained from a sample of leaves, debris and soil from a shaded area near the trap.

This was followed up two days later by direct examination in the field of moist, decaying leaves, which yielded twenty larvae. Additional larvae were found in the same area on a number of other occasions. Later a few larvae and pupae of P. pessoana (closely related to P. panamensis) were also found on decaying leaves, in two separate areas in the Madden Forest Preserve, where adults of that species were very abundant. The larvae of both species were always on moist, decaying areas of the upper and lower surfaces of the leaves, but if on the lower surfaces, then only when the leaves were lying loosely. Because of the very long caudal bristles, which in these species are held approximately perpendicular to the body, these larvae are unlikely to occur between tightly packed layers of leaves.

P. trapidoi and P. ylephiletor are also surface-feeders in the laboratory, but many searches for larvae on the forest floor in areas where adults were abundant yielded none until April-July, 1960, when particular attention was given to well-decayed leaves and leaf fragments actually on the soil surface. In this short period a total of 38 larvae and pupae were recovered from 16 out of 26 samples of this material in three different areas. The numbers in the positive samples ranged from one to six, most of them apparently either P. trapidoi or P. ylephiletor, though not all were reared for identification. All of the positive samples were from between five to ten feet from the trunks of large trees where many adults of these two species were resting. The covering of leaves in these areas was loose and in places as much as several inches thick. Samples taken at the bases of such trees have never yielded larvae of either species.

In all, 76 larvae and pupae were recovered from dead leaves on the forest floor, 39 by the flotation method and 37 by direct examination of leaves in the field. Those which were reared to the adult stage represented four species, trapidoi, ylephiletor, panamensis and pessoana.

Soil cracks. During the dry season, from about January to May, the top few inches of the soil may become hard and dry and apparently unsuitable as a larval habitat, especially on the Pacific side of Panama. However, soil cracks are also present at that time, and the more moist subsurface soil thus has direct access to the air above, which would permit adults to emerge from moist soil as well as to oviposit there. King (1914) recovered larvae in the Sudan from soil cracks, which are apparently the only breeding places in certain regions there. Attempts were made to find immature stages associated with soil cracks during the dry season of 1959 (March) at Cerro Galera, a forested area where both soil cracks and adult Phlebotomus, particularly P. sanguinarius, were abundant. The cracks here were one-half to one inch wide and at least eight inches deep. The hard clay soil had a thin covering of dry leaves, under which adults of P. sanguinarius and P. gomezi were found resting during the day. As clumps of the soil along the cracks were broken away and carefully examined, one pupal case of an unknown species was found about two inches down from the edge of one of the cracks, approximately where the soil became noticeably more moist. The specimen is unusual in that the caudal bristles of the larval exuvia are relatively short and slightly spatulate, a condition not present in any of the known reared species. To date, no more specimens have been taken in this habitat despite much searching.

Other habitats which yielded larvae or pupae were soil under overhanging roots, soil around the bases of trees and an ant nest refuse pile near a buttressed tree.

It has already been noted that Deane and Deane (1957) in Brazil obtained larvae of two species from scrapings of tree trunks. Considerable time was spent examining this possible habitat, particularly where P. ylephiletor was observed resting in large numbers; however, no immature stages were found.

While domestic or semi-domestic species occur in the Eastern Hemisphere and South America, none of the species in Panama can be so regarded. Although sandflies will often enter houses or fly under stilted shacks to bite at night, they do not remain and are seldom encountered in houses during the day, even in forested areas where they are abundant. This may be because huts in or near forests are too well ventilated, usually with many openings in the walls and under the eaves, and are thus unsuitable as daytime resting places. For this reason houses as well as animal sheds were largely unexplored as possible breeding places.

Although much is still to be learned, the general picture of sandfly breeding places in Panama has begun to take form. Four of the six man-biting species (P. trapidoi, P. panamensis, P. ylephiletor and P. pessoana) were found breeding on decaying leaves on the soil surface in well-shaded areas, with no evidence of preference for any particular spot. Whenever larvae were found, many adults of the same species were also observed nearby, either under dead leaves, on tree trunks, or on the undersides of green leaves of low plants. It seems likely that if more samples were examined, other less common species would also be found

there. The immature stages of the other two man-biting species, P. sanguinarius and P. gomezi, have not been recovered, but it is very likely that these species also oviposit on the forest floor.

In the case of a few species, particularly P. hamatus, P. ovallesi Ortiz, and P. serranus D. and A., a preference is shown for the sheltered areas between buttressed roots and at times large burrows, while the adults of these species seldom use these habitats as daytime resting places. These species, at least, thus apparently seek out such sheltered or partially enclosed places in which to oviposit rather than ovipositing at random over the forest floor.

Food of Larvae

The top layer of soil of the forest floor, especially between buttressed roots, contains feces of various animals, such as lizards, which might well be an important supply of food for Phlebotomus larvae, which, however, were not actually seen feeding on such material.

Feces of various animals have long been used for food in laboratory cultures by several workers; most species seem to prefer them over other food. Fragments of bodies of various arthropods are also numerous on the ground and on dead leaves and often make up a considerable proportion of the material taken from among buttressed roots. These fragments probably have accumulated from the predatory activities of ants, spiders, bats, etc., inhabiting these places. On one occasion larvae and pupae of P. serranus were found on a dead caterpillar taken from a dark, recessed area between buttressed roots. As all species reared in the laboratory seem to feed readily on fragments of dead insects, it is very possible that such material is generally utilized as food in natural

habitats. Soil rich in organic matter has been used satisfactorily in cultures of certain species, but most species seem to do best with feces added to the substrate.

Parrot (1932) found dead leaves sufficient for the development of P. papatasi in Algeria, and this appears to be true also for P. panamensis and P. pessoana in Panama. As discussed above, larvae of four species have been found on dead leaves and in some cases were actually seen feeding on them or on the micro-organisms growing on them. Leaf fragments are regularly included in the food used for laboratory cultures of all of the man-biting species.

It appears that all decaying organic mater, as well as mold and other micro-organisms, might readily be utilized by the larvae, judging from observations of laboratory cultures. P. panamensis has been observed feeding on moist lichens, and several species readily feed on certain molds. If crowded cultures of larvae are not provided with sufficient food, they will even devour any pupae which might be present.

Concerning the genus Nemopalpus, a large number of larvae were recovered from a soil sample taken at the base of a tree in the Cerro Azul area. The soil from the top two-inch layer contained a large amount of decayed wood, dead leaves and other organic matter. Examination of soil from similar situations on several occasions revealed no additional specimens. Adults are seen periodically during the rainy season, sometimes abundantly, in the rain forest of the Atlantic side of the Isthmus and at higher elevations on the Pacific side. They are apparently absent at lower, and thus drier, elevations on the Pacific side. It would seem that the extreme dry season there makes conditions too adverse

for larval development. Several larvae have been reared to the adult stage in the laboratory with the same food and techniques used in Phlebotomus cultures.

The exact breeding places of Warileya are still a mystery, although the environment where the adults were abundant was searched intensively. Since attempts at laboratory rearing were not successful, no clues were obtained to indicate food preferences.

Natural Enemies

No actual observations were made of any attack on Phlebotomus larvae in nature; indeed, only on a few occasions were larvae ever seen. However it would seem that they would be subject to the attack of many predators. Soil samples containing larvae very often also contained pseudoscorpions, large numbers of mites, centipedes, small ants, carabid and other small beetles and various other predatory insects. Against such predators they would be helpless, especially the non-burrowing species (P. panamensis, etc.). In laboratory cultures mites, if in large numbers, will attack the larvae and on at least one occasion a small species of ant obtained entrance and killed several larvae. Molds ordinarily are not troublesome except for certain species which produce such long, "stringy" mycelia that the caudal setae of the early instars become entangled, and particularly the genus Aspergillus, which has been proved pathogenic to the larvae (Johnson and Hertig, 1961).

Arrested Development

Diapause is well known in *Phlebotomus*, especially in the Palaearctic species, which over-winter in the fourth larval instar. It has also been reported in Brazil (Barretto, 1942), where temperature was not a factor. In cultures of Panamanian species (Johnson and Hertig, 1961), extended periods of quiescence of the fourth instar were observed in cultures which had been allowed to dry. Delayed hatching was also observed in a few species, notably *P. geniculatus*, in which on one occasion an egg hatched 30 days after oviposition (twice the normal incubation period of that species). The culture had not been allowed to dry, and other individuals developed at the normal rate.

While over-wintering is not a problem with the Panamanian species, the dry season, lasting from three to four months on the Pacific slope, has a great effect on the life history of several species. For example, adults of *P. panamensis* and *P. pessoana* are almost entirely absent during the dry months on the Pacific slope. Just which stage goes through this period is not known, but no larvae or pupae were ever recovered at this time, even in areas where these stages were found during the wet months. I believe that the egg is the most likely stage to remain during the dry season, and two facts support this hypothesis. The forest floor is extremely dry then, and larvae of these surface feeders do not resist dryness well in laboratory cultures, even though some may live for extended periods. Moreover, large numbers of adults of *P. panamensis* appear rather suddenly about one month (the normal length of time from egg to adult) after the first rains following the dry season. In 1959 frequent observations were made in an area of the Madden Forest Preserve in the Canal Zone. The first

rain at the end of the dry season occurred on April 20, with additional rain on several successive days. On June 1 large numbers of P. pessoana adults appeared and were collected, and by June 26 no more adults were seen in the area.

Adults of the species which apparently burrow into the soil may be found throughout the dry season, although usually in smaller numbers.

Pupation

In laboratory cultures, larvae about to pupate usually crawl a short distance up the sides of the container, where pupation then occurs. Often, however, it may occur on the surface of the food medium. Apparently climbing is associated with the degree of wetness of the substratum, as well as with the species. The surface-feeding species tend to climb more than the burrowing species.

Pupae were recovered from soil samples along with larvae on several occasions. However, such recoveries do not indicate their exact locations, and only by direct examination in the field can this be determined. Judging from laboratory cultures, it would seem that pupation would occur at the surface of the soil or above it, on leaves, tree trunks, rocks, etc. Pupal cases were found in the field on three occasions: one near the edge of a crack in the soil, one on the underside of a rock a short distance from the soil surface, and one on the underside of a loose, dead leaf.

SYSTEMATICS

Previous Descriptions of Immature Forms

Since Grassi's pioneering work on the immature stages of Phlebotomus appeared in 1907, in which the immature stages were described and figured for the first time, there have been several papers published on the taxonomy and morphology of the immature stages of this genus. Most of these, however, are descriptions of one or a few species. Newstead (1911) described and illustrated the egg, larval and pupal stages in his treatment of the Maltese species. Patten and Hindle (1928) differentiated the three species occurring in China, as did Smith, Krishnan and Mukerjee (1934) with three other species in India. Other workers treating Palaearctic species were Colas-Belcour (1928), Schevtschenko (1931), and Sacca (1950, 1952). A notable series of papers by Abonnenc (1956a, 1956b) and Abonnenc and Lariviere (1957) contain descriptions and illustrations of nine species from North Africa. The important characters differentiating these species, especially the nature of the setae, are shown in detail.

In the Western Hemisphere, the important works of Barretto (1940, 1941) and Mangabeira (1942a-f) have done much to make known the neotropical species. Barretto (1941) described and figured the immature stages of ten species occurring in Brazil, and Mangabeira, in his series of papers, added five more. More recently, Sherlock (1957a, 1957b) and others have continued to describe additional species from Brazil. Mirsa (1952) described the immature stages of two species occurring in Venezuela. In the United States, three species have been described in papers by Lindquist (1936), Addis (1945) and Chaniotus and Anderson (1964).

The immature stages of the genus Bruchomyia were first described and illustrated by Satchell (1953).

In summary, descriptions and illustrations of larval stages of the following species of Phlebotominae have been published:

Eastern Hemisphere

Phlebotomus--antennatus occidentalis, argentipes, ariasi, dubius, freetownensis sudanicus, longicuspis, magnus, major chinensis, minutus, papatasi, parroti, perfiliewi, perniciosus, schwetzi, sergenti, taianensis

Western Hemisphere

Phlebotomus--alphabeticus, anthophorus, arthuri, avellari, bahiensis, brasiliensis, diabolicus, fischeri, gomezi, guimaraesi, intermedius, lanei, lenti, longispinus, migonei, monticolus, oswaldoi, panamensis, pestanai, renei, shannoni, travassosi, triacanthus, vexator occidentis

Bruchomyia--argentina

Preparation of Specimens

Rearing of larvae

Several of the species included in this study were obtained from cultures being maintained at the Gorgas Memorial Laboratory, which originated from adult females collected from man or horses. Nearly all of the remaining non-man-biting species were obtained by me during the course of field studies. Gravid or engorged females were constantly sought and returned to the laboratory in plaster-lined aspirator tubes kept cool and moist. Upon arrival at the laboratory, each specimen was isolated in a 5-dram, plaster-lined vial (as described by Hertig and

Johnson, 1961), which was kept on moist cotton until oviposition. Food consisting of ground rabbit feces, leaf fragments and dead insects was added just before the anticipated time of hatching. The entire rearing process took place within the same vial. Since the mature larva was the main object of the rearing, that stage was the first of each species to be preserved. Only when mature larvae became available were earlier stages removed and preserved. Thus, where only a few eggs hatched, the earlier stages were not preserved.

Mounting. In order for correct identification to be made, it is important that extreme care be taken in the preparation of mounted specimens. Not only is it necessary to observe the nature of body bristles, but their positions on the body must be readily seen. The bristles are fragile and easily dislodged, and if the body has become distorted, it is usually impossible to interpret them accurately.

A number of different mounting techniques were tried. The usual methods, which involve passing the specimen through a series of increasing concentrations of alcohol, usually resulted in considerable breakage of body bristles and distortion and shriveling of the body. The use of cedarwood oil for clearing and dehydrating invariably resulted in collapse of specimens when they were transferred to balsam. Phenol was found the most satisfactory dehydrating agent when mixed with an equal amount of xylol to prevent crystalization in a dry atmosphere. The method used is as follows:

The specimen is placed in 10% KOH at room temperature and left overnight, or in hot KOH for several minutes. While it is in the KOH, the body wall is punctured ventrally behind the head capsule and in the abdominal region. The specimen is then pumped gently, so that as much

as possible of the macerated material within the body is removed. The gut contents can seldom be removed in this way without damage to the bristles, and although the final mount has a better appearance without this material within the body, it is not a serious obstruction. The specimen is transferred directly to a mixture of equal amounts of phenol and xylol and left about one-half hour, or until the KOH within the specimen has been completely displaced or neutralized. Although rinsing in water after the KOH treatment would seem more desirable, the specimens thus treated always become distorted and many of the bristles dislodged. Fresh phenol-xylol must be used after every few specimens; otherwise, subsequent specimens will not stain satisfactorily. The specimen is placed in stain and left until sufficiently stained. About twenty minutes in acid fuchsin dissolved in phenol-xylol was found adequate. It is then transferred to xylol and carefully pumped to eliminate the stain solution within the body. Since xylol causes brittleness, extreme care must be taken in transferring and handling the specimen. The specimen is transferred to thin balsam, allowing the balsam to slowly infiltrate the specimen, which would collapse if placed directly into thick balsam. The specimen is mounted on a coverslip and left to dry partially, after which the coverslip is turned over onto a drop of balsam on a slide. Small pieces of glass are placed under the edges of the coverslip to prevent any distortion of the specimen by the weight of the coverslip or shrinkage of the balsam in drying.

Morphological Characters Used

Antennae (Plate 1, fig. a)

Unlike the species of the Eastern Hemisphere, those of the American continents exhibit considerable variation in the form and position of the antennae. In those species that burrow in their food medium in laboratory cultures (and probably in the soil in their natural habitat), the antennae are short and, in some species, somewhat appressed. In the surface-feeding species, however, the antennae are erect and often on prominent tubercles. This feature is exhibited in its most extreme form in P. apicalis. Although generally regarded as being three-segmented, the antennae actually appear two-segmented when highly magnified. What had been supposed to be the first segment is apparently an outgrowth of the head capsule and is best seen in the surface-feeding species. This outgrowth is here called the antennal tubercle. The actual first segment is usually short and more slender than the apical segment, but in some species it is longer than wide and may be considerably longer than the apical segment. In others the apical segment is slender and strongly curved posteriorly.

Integument of head capsule

The surface of the head capsule bears minute spicules, the arrangement of which gives an imbricated effect, especially posteriorly. This character has limited use because of the difficulty of describing spicular arrangement and the lack of precise differences among closely related species. There is also considerable individual variation. The coloration of the head capsule varies from pale gray, as in P. apicalis, to dark brownish black, as in P. sanguinarius. In P. geniculatus the head is strikingly bicolored, with pale antennal areas and the remainder of the head brown.

Setae (Plate 1)

The nature and position of the setae have long been recognized as valuable tools in differentiating species of Phlebotomus. Colas-Belcour (1928) was apparently the first to provide a system of nomenclature for the body setae, but the more complete and applicable nomenclature of Barretto (1941) is largely followed in this study.

Abonnenc (1956) devised a numerical system for the setae, as has been done for mosquito larvae. This may eventually prove to be the most desirable system, but it would probably have to be revised, as certain setae given the same numbers on adjacent segments are probably not serially homologous. For example, his seta 5 of the prothorax is quite different from seta 5 of the mesothorax. The dorsal head setae (posterior and exterior frontals and lateral and dorsal verticals) are the most useful in species differentiation. They may be long and simple at one extreme to short and brush-like at the other. The relative positions of the lateral and dorsal verticals are also of some value in differentiating certain species.

The dorsal and lateral setae of the thorax and abdomen may vary in length, position, and nature and are very important in species determination. The ventral setae are short and inconspicuous and have not been found taxonomically useful, although no great effort was made to find differences. The prothorax bears two transverse rows of dorsal setae, thus differing from the meso- and meta-thorax, each of which bears only one row. The two mesal pairs are the "dorsal setae"--internal and external. In a few species the anterior row of prothoracic setae includes only one pair of dorsals. In this row the internal dorsals are always longer than the external dorsals, whereas the opposite is

true in the posterior row. Lateral from the external dorsal is the laterodorsal seta. There is an anterior as well as a posterior laterodorsal on each segment. On the pleural region and ventral to the laterodorsal is the lateroventral, which is usually long and conspicuous.

The abdominal setae can generally be homologized with those of the thorax, but a few problems exist with those of the eighth abdominal segment. It is questionable whether the seta just posterior to the spiracle is really the external dorsal or the laterodorsal. In most species it is long and very similar to the laterodorsal of the preceding segment (Plate 2, fig. e), but in some species it is very short like the internal dorsal (Plate 10, fig. d). In this study I have called it the external dorsal, following Barretto. Each of the first seven segments of the abdomen bears a pair of short setae anterior to the dorsals. These are termed intersegmentaries by Abonnenc and are usually extremely short and inconspicuous. However, in species of the subgenus Brumptomyia, they are more than half the length of the dorsals of the same segment (Plate 7, fig. c).

The long setae at the posterior end of the abdomen are termed caudal setae; these are characteristic of the genus. Two pairs are present in all species, except those of the subgenus Brumptomyia, in which only one pair is present. These setae may be longer than the body in the surface-feeding species, whereas in the burrowing species they are usually much shorter than the body. The inner pair are always longer than the outer pair.

The coloration of the setae may also vary. Those setae which are completely brush-like from base to apex are yellowish, while those which are simple or partly brush-like are sometimes dark. In P. sanguinarius

and P. hartmanni, in which only the apical halves of the setae are brush-like, the basal halves are dark and the apices yellow.

Classification

While the Old World species are not dealt with here, it should be pointed out that they, unlike the New World species, are rather well known, and a sound system of classification has been developed for them by Theodor (1948). In nearly all of those species both sexes of adults have been described, and relatively few new species are being discovered. In contrast, of the approximately 250 New World species, about 100 are known from only one sex, and new species are being described each year.

No general classification of the American species had been proposed until the works of Barretto (1955) and Fairchild (1955). Barretto recognized two general, Brumptomyia Franca and Parrot and the Old World genus Sergentomyia Franca and Parrot, but later, in 1961, considered Lutzomyia Franca to include those species which he formerly placed in Sergentomyia. In 1962 he recognized 15 subgenera of Lutzomyia, eight of them new. Fairchild proposed a classification on a worldwide basis, in which the above generic names are given no higher rank than subgeneric status within the genus Phlebotomus. In the Tribe Phlebotomini he included three genera, Phlebotomus, Warileya and Hertigia, and recognized three subgenera, Psychodopygus, Viannamyia and Brumptomyia, and several groups and series for the New World species of Phlebotomus. The Old World species comprised the two subgenera Phlebotomus and Sergentomyia. The genera Bruchomyia Alexander and Nemopalpus Macquart, generally considered to comprise a separate subfamily, were placed in the Tribe Bruchomyini

within the subfamily Phlebotominae. A number of the groups and series, especially in Brumptomyia, were acknowledged to be highly tentative.

In 1965 Theodor carried out a comprehensive analysis of the New World species in an attempt to establish a classification correlated with hat of the Old World species. He showed that in the New World species there is a characteristic bulge dorsal to the cibarium of the adult, which is not present in the Old World species. Mainly on this basis he removed all of the New World species from the genus Phlebotomus, placing most of the species in the genus Lutzomyia, and the remaining, those with only two caudal setae in the larval stage, in the genus Brumptomyia. Subgenera, groups and series were also used, which followed, to a large extent, Fairchild's arrangement. Since it was acknowledged to be a provisional classification, no new names for categories were proposed. Subgeneric names already published were used for groups which were given a rank equal to species groups.

It is, I believe, unfortunate that the genus Phlebotomus has been divided into separate genera, as, if Theodor's system is accepted, it would require a change in the generic names of all of the American species. Several of these names have been used extensively in literature, especially those of species involved in disease transmission, and confusion very likely would result. While the New World species probably form a group, or groups, distinct from those of the Old World, it would seem that these groups might just as well be considered as subgenera. Theodor believes that the level of subgenus does not "express its separate position clearly enough," but, on the other hand, the placing of segments of Phlebotomus at the same level as the genera Warileya and Hertigia obscures the wide gap existing between Phlebotomus and those two genera.

An overabundance of generic names exists for closely related groups of species. In most cases these should represent only series or groups, as treated by Theodor.

In as much as the above classifications were based on adult characters, and chiefly on characters of the male genitalia and of the spermathecae, it was hoped that characters of the larval forms could be found which would help to show the relationships within the genus Phlebotomus. However, before a complete classification based on larval forms can be undertaken, larvae of additional American species will have to be studied. To date, larval forms of only about one-fifth of the more than 200 American species are known. Nevertheless, on the basis of the available species some general groupings can be set up. Based on larval characters alone, the genus can be subdivided into a few well-defined groups. P. galindoi and P. hamatus, two closely related species, show the greatest departure from the others and probably deserve subgeneric ranking. They possess only one pair of caudal setae instead of the usual two pairs; the antennae are strongly directed forward, and the apical segment of each is somewhat acute distally; the intersegmentary setae are long, at least half the length of the dorsal setae. The brushlike setae also show a transparent globule at the apex, similar to the condition in Nemopalpus. The name Brumptomyia therefore would be limited to Series brumpti of Fairchild's classification.

The remaining species, with a few exceptions, seem to fall into two groups, as follows:

Group 1. The antennae are at the approximate level of the anterior frontals and not on large tubercles; the internal and external dorsals vary in length, but never are all of them short; the caudal setae are never as long as half the body length; the body is cylindrical and pale, except for the head capsule, which may be brown to nearly black. These readily burrow beneath the surface of the food material in laboratory cultures and probably also in the soil under natural conditions.

Group 2. The antennae are well behind the anterior frontals and situated on tubercles; the internal and external dorsals are short in comparison with the lateral setae; the caudal setae are very long, more than half the length of the body; the body is more or less depressed and, in some species, dark gray or tan. These are surface-feeders and probably do not burrow in the soil.

Species difficult to place are P. gomezi, P. vexillarius, P. vespertilionis, and P. spinosus. The first two seem to be closely related and are placed in a separate group. In these two species the external dorsals are strongly directed forward, in contrast to the internal and laterodorsals, which are directed backward. The antennae are similar to those of group 2, in that they are behind the anterior frontals and are erect. The apical segment is strongly curved backward. The posterior lateroventrals of the abdomen are simple setae, not brush-like. The larvae are surface feeders but are not noticeably flattened dorsoventrally, as are those of group 2.

In P. verpertilionis the antennae are in line with the anterior frontals and not on enlarged tubercles, as in group 1, but they are erect, and the apical segment is longer than wide, unlike any of those

in group 1. The internal and external dorsals of the abdominal segments are very short, as in most species of group 2.

P. spinosus is difficult to place in any of the above groups, although it is similar to group 2 in that the antennae are erect and arise from moderate-sized tubercles. It is apparently also a surface feeder. However, the dorsals of the thorax and anterior abdominal segments are rather long.

In plate 27 the larval classification is compared with Fairchild's classification based on adult characters. A few striking discrepancies are evident. Fairchild's series brumpti (containing P. galindoi and P. hamatus) is a distinct subgenus in the larval classification, as already discussed. His group shannoni, one species of group cruciatus, and subgenera Viannamyia and Psychodopygus comprise group 2 in the larval classification. Adults of these species also agree in several characters. The fifth palpal segment is rather short, the male gonostyli possess four spines and no subterminal setae, the coxites are without definite tufts, and in the females of most of these species the cibarium possesses more than four teeth. Although species placed in group 1 of the larval classification are rather diverse with regard to adult characters, none of them possesses the combination of characters listed above.

The genera Bruchomyia and Nemopalpus are usually placed in a separate subfamily of the Psychodidae, the Bruchomyiinae. The discovery of Marileya by Hertig (1948) and Hertigia by Fairchild (1949), which possess characters of both Bruchomyiinae and Phlebotominae, has somewhat broken down the distinction between these two subfamilies. Fairchild (1955) discussed in detail the relationships of these genera based on adult characters.

The immature stages of Bruchomyiinae were unknown until Satchell's description of those of Bruchomyia argentina Alexander (Satchell, 1953).

He pointed out the close similarity between the immature stages of this species and those of Phlebotomus and stated, "Were the placing of Bruchomyia to depend only on the evidence supplied by a study of the early stages, there is little doubt that it would be placed as another genus within the Phlebotominae." He retained Bruchomyiinae because of such adult differences from Phlebotominae as the absence of haematophagous mouthparts and the dichotomous instead of pectinate radial sector. However, Hertigia, in which haematophagous mouthparts are present, shares with Bruchomyia the character of a dichotomous radial sector.

Aside from morphological characters, there is a close similarity between adult Phlebotomus and Nemopalpus (which is close to Bruchomyia) in general habits, such as pattern of flight and the position of the wings and abdomen while at rest. I have observed the flight of Nemopalpus on numerous occasions, and the undulating pattern was strikingly similar to that of Phlebotomus. In fact, at first glance Nemopalpus looks very much like a large Phlebotomus. The wings are held above the abdomen, as in Phlebotomus, in an approximately horizontal position, and not roof-like over the abdomen as in genera of Psychodinae.

Striking differences between Bruchomyiinae and Phlebotomus are seen in the male genitalia and spermathecae in the adults. In larval Bruchomyiinae abdominal pseudopods are absent, the antennae do not project from the head capsule, and eye spots are present.

Thus, while there are distinct differences in both the larval and adult stages of Bruchomyiinae and Phlebotominae, these two groups are so much closer to each other than to other subfamilies of Psychodidae that it seems best to place them in separate tribes within the subfamily Phlebotominae.

The following classification includes all New World species of which the fourth instar larva has been described.

Subfamily Phlebotominae

Tribe Phlebotomini

Genus Phlebotomus

Subgenus Brumptomyia

avellari, galindoi, guimaraesi, hamatus, travassosi.

Subgenus Lutzomyia

Group 1. anthophorus, bahiensis, camposi, cayennensis dysponetus, hansoni, hartmanni, lenti, longispinus, odax, oswaldoi, ovallesi, pinealis, reni, rubidulus, sanguinarius, serramus, triacanthus, trinidadensis, triramulus, vexator.

Group 2. aclydiferus, alphabeticus (?), apicalis, arborealis, arthuri, barrettoi, brasiliensis, carpenteri, dasymerus, geniculatus, intermedius, lanei, panamensis, pessoana, pestanai, runoides, shannoni, trapidoi, whitmani, ylephiletor.

Group 3. gomezi, vexillarius.

Group 4. vespertilionis, isovespertilionis.

Group 5. spinosus.

Unplaced species. fischeri, migonei, monticolus.

Genus Warileya.....rotundipennis.

Tribe Bruchomyini

Genus Bruchomyia...argentina

Genus Nemopalpus...sp.

Genus Phlebotomus
Fourth Instar Larva

The genus has been described and the characters discussed by several writers. A brief summary of the larval characters is as follows:

Head well developed, strongly sclerotized, usually brownish; antennae apparently two-jointed, the first segment narrow, varying in length from a short ring to several times its width; second, or apical segment, wider than first segment and somewhat flattened, bearing a very small, slender, terminal seta; eye spots absent; posterior head setae usually branched or brush-like, some setae with at least minute branches toward apices; integument with microsetae, often giving an imbricated effect; clypeus narrow, continuous with frons, bearing a pair of setae basally and a pair distally; labrum transparent, non-sclerotized, minutely rugose and bearing several peg-like microsetae; mandible strongly sclerotized, with four rounded teeth and two long and one very short setae near base; maxillae non-sclerotized, somewhat rectangular, bearing a few setae on outer surface and many minute spines along distal edge; maxillary palpus short, one-segmented, bearing several minute, peg-like structures; hypostome strongly sclerotized, with four pairs of rounded teeth, the middle pair longest. Thorax and abdomen usually pale and unicolorous; integument conspicuously folded, covered with microspines or tubercles; nearly all setae brush-like or at least with minute branches; prothorax with two transverse rows of setae, anterior row with two or three pairs of dorsal setae, posterior row always with three pairs; meso- and meta-thorax with only posterior row present, except for anterior lateral seta; abdominal segments I-VII with setae as in meso- and meta-thorax, with addition of pair of anterior

dorsals (intersegmentaries); a simple, slender seta also present laterally on each pseudopod; abdominal segment VIII complex, consisting of large anterior region, anal region, and caudal region bearing long caudal setae. (Latter two regions may represent segments IX and X.) Caudal setae very long, from one-third length of body to more than its length, one or two pairs present; abdominal segments I-VII and anal region of segment VIII with ventral pseudopods, no crochets present; segment VIII with dark patches dorsally, especially dark on caudal protuberances; one pair of small spiracles on posterior edge of prothorax and one larger pair on segment VIII of abdomen.

Early Larval stages

Second and third instars very similar to fourth but generally lack pigmentation on dorsum of eighth abdominal segment. Setae shorter and weaker. First instar differs somewhat more, as follows: Conspicuous egg-tooth on posterodorsal region of head, setae generally more slender, only one pair of dorsals present in anterior row of prothoracic setae, only one pair of caudal setae present.

Pupa

Coloration pale tan to yellowish buff. Head region well-differentiated, with prominent frontal area. Thoracic region prominent, keeled dorsally, with an anterior and a posterior swelling. A pair of prominent lobes, varying in size according to the species, situated between the two swellings. Respiratory horn not conspicuous, in form of short lobe at anterior base of wing. Pre-alar lobe posterior to respiratory horn, bearing two or three very short to long spines. Wing lobe gently curved, the tip acute. Abdominal segments with

prominent tubercles, each bearing a short seta. Several microsetae scattered over head, thorax and abdomen. Abdomen usually curved, so that thorax protrudes conspicuously backwards. Terminal abdominal segments remain within larval skin, which is adhered to substratum.

The following key pertains to the fourth instar larvae of only those species of which specimens are at present available. Nevertheless, it includes all of what might be considered the common species, and it might serve as a guide for future work when more of the species are known. It will also be noted that certain pairs of species cannot yet be differentiated in the larval stages.

Key to the Fourth Instar Larvae of the *Phlebotomus* of Panama

1. One pair of caudal bristles present; intersegmentaries of abdomen at least half as long as other dorsal setae. . . . . (*Brumptomyia*) . . . . . *galindoi*

hamatus

Two pairs of caudal bristles present; intersegmentaries of abdomen much less than half as long as other dorsal setae 2

2. Antennae situated high on head, well behind anterior frontals (if somewhat close to anterior frontals and apical segment is strongly curved backward, see *gomezi*) 13

Antennae situated anteriorly, about at level of anterior frontals. Apical segment of antenna not curved backward . 3

3. Antennae extending upward, perpendicular to head 4

Antennae extending forward from head 5

4. Internal and external dorsals of third abdominal segment very short . . . . . vespertilionis

isovespertilionis

Internal and external dorsals of third abdominal segment not much shorter than laterodorsals . . . . . spinosus

5. Internal dorsals of third abdominal segment short, half as long as external dorsals or less 6

Internal dorsals of third abdominal segment long, more than half length of external dorsals 11

6. External dorsals of eighth abdominal segment several times longer than internal dorsals 7

External dorsals of eighth abdominal segment very short, equal in length to internal dorsals 8

7. Head with posterior frontals situated posterior to dorsal verticals; internal dorsals of third abdominal segment very short . . . . . ovallesi

Head with posterior frontals situated anterior to dorsal verticals; internal dorsals of third abdominal segment about half length of external dorsal . . . . cayennensis

8. Head with posterior frontals situated posterior to dorsal verticals . . . . . rubidulus

Head with posterior frontals situated anterior to dorsal verticals 9

9. Posterodorsal head setae brushlike, clavate; thoracic and abdominal setae uniformly pale . . . . . trinidadensis

Posterodorsal head setae with only sparse branches not brushlike; thoracic and abdominal setae with basal halves dark, the ends pale 10

10. Anterior external dorsal of prothorax more than half length of anterior internal dorsal . . . . . sanguinarius

Anterior external dorsal of prothorax less than half length of anterior internal dorsal . . . . . hartmanni

11. Posterior internal dorsal of prothorax about equal in length to external dorsal . . . . . serranus

Posterior internal dorsal of prothorax not more than 2/3 length of external dorsal 12

12. Internal dorsal of mesothorax very long, nearly 3 times length of posterior internal dorsals of prothorax. triramulus

Internal dorsal of mesothorax less than twice length of posterior internal dorsals of prothorax . . . . dysponetus camposi

13. External dorsal directed strongly forward, in contrast to internal dorsals 14

External dorsal not directed forward, but oriented in same direction as internal dorsals 15

14. Internal dorsal of 8th abdominal segment about 1/4 length of external dorsals; head capsule dark brown . . .vexillarius

Internal dorsal of 8th abdominal segment 1/3 to 1/2 length of external dorsals; head capsule light brown . . . . gomezi

15. Prothorax with only one pair of anterior dorsals . . 16

Prothorax with two pairs of anterior dorsals 20

16. Apical segment of antennae distinctly curved backward 17

Apical segment of antennae not curved 18

17. Posterior dorsals of prothorax about equal in length . . . . . ylephiletor

External posterior dorsals of prothorax about twice length of internal dorsals . . . . . trapidoi

18. Head capsule largely brownish 19

Head capsule wholly whitish . . . . . panamensis pessoana

19. Head capsule wholly brownish . . . . . aclydiferus

Head capsule bicolored, large antennal tubercles and adjacent ventral areas whitish, remainder brown . . geniculatus

20. Head and prothorax whitish, remainder of body dark gray; antennal tubercle large, longer than antenna, which is distinctly perpendicular . . . . . apicalis

Head brown, thorax and abdomen white or pale tan; antennal tubercle shorter than antenna, or antenna distinctly directed backward 21

21. Penultimate antennal segment longer than apical segment, which is not curved posteriorly . . . . . shannoni

Penultimate antennal segment shorter than apical segment, which is curved posteriorly 22

22. Anterior external dorsals of prothorax about half length of anterior internal dorsals, not in line with internal dorsals and laterodorsals and situated posteriorly from them . . . . . arborealis

Anterior external dorsals of prothorax very short, knob-like and situated in line with internal dorsals and laterodorsals . . . . . runoides

Phlebotomus aclydiferus Fairchild & Hertig

(Plate 2)

Fourth instar larva

Average length 3.25 mm. Six specimens.

Head. Fronto-vertical profile rather evenly rounded; antennal tubercle prominent, directed slightly backward, situated close to level of posterior frontal seta, as seen in lateral aspect; first antennal segment much longer than wide; apical segment about equal in length to first segment, directed backward at slight angle; integument covered with spicules, some strongly curved forward, others arranged in curved rows posteriorly.

Thorax and abdomen. Somewhat depressed. Prothorax and ventral surface of thorax and abdomen covered with spicules; pleural region and dorsum of mesothorax, metathorax and abdomen with conspicuous tubercles, some of those on summits of folds strongly curved forward, especially on meso- and meta-thorax.

Coloration. Head brown, thorax and abdomen whitish with dark brown patch on dorsum of segment VIII and caudal protuberances.

Chaetotaxy. Head--Posterior frontals shorter than other cephalic setae, with short branches on distal half. Other setae acuminate, with only minute, sparse branches distally. Anterior frontal very long. Prothorax--Setae on prominent tubercles. Only one pair of anterior dorsals present, branched along distal two-thirds anterior laterodorsal similar; anterior lateroventral slightly longer. Posterior internal dorsal very small, rounded and branched at apex, directed anteriorly; posterior external dorsal greatly expanded at apex; posterior laterodorsal distinctly longer than external dorsal

~~distinctly longer~~; posterior lateroventral slender, less than half length of lateroventral. Meso- and meta-thorax--Internal dorsal small, directed slightly posteriorly, truncate and brush-like at apex. External dorsals somewhat longer but similar; laterodorsal considerably longer, branched along two-thirds its length; anterior lateroventral about one-third longer than laterodorsal, similarly branched; posterior lateroventral slender, less than half length of anterior lateroventral. Abdomen--Dorsals smaller than those on thorax, diminishing in size posteriorly. Laterodorsals long, same length throughout abdomen. Anterior and posterior lateroventrals about equal in length to laterodorsal. Intersegmentaries small. Internal dorsal of segment VIII very small; external dorsal long, at least as long as laterodorsal and similarly branched. Lateroventral three-fourths length of laterodorsal. Caudal setae 2.9 mm. long, two pairs present. Internal postanal short, straight. External postanal long and whip-like.

Pupa

Average length 2.8 mm. Six specimens. Respiratory horn long and tapering. Prealar lobe prominent, two apical setae straight, heavy. Mesonotal tubercle conspicuous, longer than wide.

Discussion

I have not observed this species in cultures, but the long caudal setae and general body form indicate that it is surface-feeding in habits. It has not been recovered from natural habitats. The larva seems closest to that of P. trapidoi and P. ylephiletor. It may be distinguished from them by the less curved antennae, the two segments of which are about equal in length, and by the much longer posterior lateroventrals of the thorax.

Phlebotomus apicalis Floch & Abonnenc

(Plate 3)

Fourth instar larva

Average length 3.6 mm. Fourteen specimens.

Head. Globose, the frontal region very prominent. Fronto-clypeal furrow deep; posterior clypeal region strongly produced. Antennal tubercle extremely long, arising perpendicularly from head midway between anterior and posterior frontal setae. First segment of antenna longer than wide. A small and narrower ring at apex of segment gives an impression of additional segment. Apical segment narrow, about same width as first segment and slightly longer, the two segments nearly in a straight line. Integument covered with small, strongly curved spicules, not arranged in definite imbricated design.

Thorax and abdomen. Somewhat depressed, elongate. Integument with spicules or tubercles, the latter predominant on dorsal and pleural regions. Tubercles rounded, with ridged slopes.

Coloration. Head grayish white dorsally, darkened ventrally. Prothorax whitish, contrasted with mesothorax and posterior segments, which are dark gray. Dorsum of eighth abdominal segment without dark patch on anterior section; caudal protuberances with brownish black patch.

Chaetotaxy. Head--All setae acuminate, darkly colored, only minutely branched, the branches more conspicuous on dorsal vertical; posterior frontal strong, longer than other setae; dorsal vertical rather short. Prothorax--Anterior internal and external dorsals and anterior laterodorsal darkly colored, slender, blunt, inconspicuously branched; anterior lateroventral long, acuminate, pale;

posterior dorsals and laterodorsal similar in structure and coloration to anterior setae; posterior lateroventral dark, about one-third length of anterior lateroventral. Meso- and metathorax--Setae as on posterior prothorax, but directed posteriorly; both anterior and posterior lateroventral long, acuminate, nearly equal in length, both situated on single, large, lateral swelling, anterior laterodorsal slightly ventrad to posterior lateroventral. Abdomen--Dorsals progressively shorter toward posterior end; laterodorsals dark, long and conspicuous, acuminate, strongly curved backward; anterior and posterior lateroventrals pale, acuminate, about equal in length, and directed ventrad; intersegmentaries small. On segment VIII, internal dorsal very short, pale; external dorsal long, dark, acuminate, similar to laterodorsal on previous segment; laterodorsal and lateroventral nearly equal in length, the latter slightly shorter. Two pairs of caudal setae present, length 3.3 mm.; external postanal long, whip-like.

First instar larva

Head. Frontal profile less prominent than in fourth instar. Antennal tubercle large, but shorter than antenna. Thorax and abdomen. Coloration light gray. Setae relatively long and strong, especially laterodorsals and lateroventrals. Dorsals rather short, as in fourth instar. Caudal setae much longer than body. Three specimens.

Pupa

Average length 3.0 mm. Two specimens. Respiratory horn longer than wide; pre-alar lobe conspicuous, the spines rather weak; mesonotal tubercle acute and prominent; all three structures directed strongly anteriorly.

Discussion

The mature larva of this species is very distinctive in its coloration and form. The pale head and prothorax contrast with the dark gray of the rest of the thorax and the abdomen. The globular head and conspicuous antennal tubercles are also distinctive. The long caudal setae are held vertically. A surface-feeder, it is a slow-moving species, usually stationary as long as food is present. The immature stages were not found in nature but probably inhabit moist leaf litter in heavily forested areas. It is rather easily reared in the laboratory on food consisting of decayed leaves, sheep feces and dead insects.

Phlebotomus arborealis Floch & Abonnenc

(Plate 4)

Fourth instar larva

Average length 3.1 mm. Six specimens.

Head. Ovoid, the frontal region prominent. Antennal tubercle prominent, well posterior to anterior frontal setae, directed somewhat posteriorly. First segment of antenna slightly longer than wide, less than half as long as second segment, which is about equal to first segment in width and strongly curved in middle, the apex directed posteriorly. Integument covered with spicules, which are not curved at apices; on posterior region spicules arranged in irregular circles, no imbricated arrangement.

Thorax and abdomen. Somewhat depressed and robust. Integument covered with curved spicules, which on dorsal folds are replaced by rounded tubercles. Setae arise from prominent tubercles.

Coloration. Head dark brown; thorax and abdomen light tan; dorsum of segment VIII of abdomen with large brown patch, caudal protuberance dark brown; sides of posterior section of segment VIII with a few darkened areas.

Chaetotaxy. Head--Posterior frontal and dorsal vertical blunt, sparsely branched on distal half; anterior frontal and lateral vertical acuminate and simple except for minute sparse branches visible only under high magnification. Prothorax--Anterior interior dorsal prominent, slightly clavate, brush-like on distal half; anterior external dorsal smaller, about half as long as, and distinctly posterior to, anterior internal dorsal; anterior laterodorsal similar to internal dorsal; anterior lateroventral slightly declinate, sparsely branched, not clavate but blunt; posterior dorsals clavate, erect, the internal dorsal smaller than external one; posterior lateroventral very short. Meso- and metathorax--Dorsals and laterodorsal as in prothorax but somewhat reclinate; anterior lateroventral declinate, blunt; external ventral also declinate and similar to anterior lateroventral, but shorter. Abdomen--Dorsals like those of metathorax but shorter and more reclinate; laterodorsal slightly longer than that of metathorax; anterior lateroventral similar in length to and posterior lateroventral about twice length of corresponding setae of metathorax; intersegmentaries very short. Segment VIII with external dorsal and laterodorsal long, equal in length. Two pairs of caudal setae present, length 2.1 mm. External postanal rather long, whip-like; latero-anal similar to it but smaller.

First instar larva

Head. Antennal tubercle prominent. Antennae erect; apical segment more than twice length of basal segment, directed slightly backward. Anterior frontal very long, simple; posterior frontal blunt, slightly branched at apex. Two specimens.

Pupa

Average length 2.2 mm. Four specimens. Respiratory horn not slender, rather inconspicuous; pre-alar lobe directed forward; mesonotal tubercle longer than wide.

Discussion

This species is similar in general appearance to P. trapidoi and P. ylephiletor, but it possesses both the internal and external dorsals in the anterior row of prothoracic setae, although the external dorsal is small and noticeably posterior to the others in the row. It is a slow-moving species and remains stationary for long periods while feeding. The caudal setae are "flicked" at any slight disturbance. Although the larva will readily crawl partly into the food material, it is basically a surface-feeder, and the long, vertically held caudal setae always remain exposed. It will feed on decayed leaves but seems to prefer insect fragments. The larvae have not been found in nature, and although adults (including gravid females) were taken from a tree hole on several occasions, no larvae were recovered there.

Phlebotomus barrettoi Mangabeira

(Plate 25, Fig. f)

First instar larva

Head. Antennal tubercle produced but not prominent. Antenna straight, directed slightly posteriorly, apical segment several times longer than basal segment. Anterior frontal slightly branched on apical third; posterior frontal short, blunt, branched only on apical half; lateral vertical much longer than posterior frontal branched on apical half, blunt; dorsal vertical short, branched throughout length. Thorax and abdomen--Anterior prothoracic dorsals brush-like, expanded apically; remaining dorsals very short; lateral setae long, branched on apical half; caudal setae much longer than body length. One specimen.

Discussion

This species is obviously closely related to P. carpenteri and P. runoides, as shown by the rather short posterior frontal and dorsal vertical and the short, brush-like dorsals. The position and form of the antennae are also similar. It is nearly identical to P. carpentari, but the lateral body setae appear to be branched only on the apical half, whereas in P. carpenteri they are branched along most of their length. This character, however, may not prove significant when many specimens are examined. Neither species could be reared beyond the first instar, as they refused to feed on the food (feces and dead leaves) available to them, but continually crawled over the food until they died. The body form and long caudal setae indicate a surface-feeding habit.

Phlebotomus camposi Rodriguez

(Plate 5)

Fourth instar larva

Average length 2.8 mm. Two specimens.

Head. Fronto-vertical region not strongly produced. Antennal tubercle small, situated slightly anterior to anterior frontal setae. Antenna directed forward; first segment small, shorter than wide; apical segment ovoid, much wider and longer than first segment. Integument covered with spicules curved forward, arranged in curved lines laterally and posteriorly, giving imbricated effect.

Thorax and abdomen. Nearly cylindrical. Integument covered with short microtubercles and spines. All dorsal setae strongly clavate.

Coloration. Head brown, dorsal oral margin darker. Thorax and abdomen whitish. Dorsal abdominal brown patches on segment VIII conspicuous. Caudal protuberance dark brown.

Chaetotaxy. Head--Anterior and posterior frontals and dorsal and lateral verticals brush-like, anterior frontals slender. Prothorax-Anterior internal dorsal strongly clavate, about twice as long as anterior external dorsal; posterior internal dorsal considerably shorter than external dorsal. Meso- and metathorax--Internal dorsal nearly as long as external dorsal, but longer than internal dorsal of prothorax. Setae otherwise like those of posterior prothorax. Abdomen--Segments I-VI with dorsal and lateral setae about equal in lengths; internal dorsal of segment VII very short and inconspicuous; intersegmentaries very short. Segment VIII with external dorsal longer than laterodorsal; internal dorsal short and inconspicuous. Two pairs of caudal setae present, length 1.2 mm. External postanal about twice length of internal postanal.

Discussion

In this species the antennae are situated anteriorly. It is very similar to P. triramulus and P. serranus in that the internal dorsals of the anterior segments of the abdomen are long. It may be distinguished from these by the relative lengths of the internal dorsals of the prothorax and mesothorax, as given in the key. In P. triramulus the dorsals are very long. P. camposi readily crawled beneath the material in the laboratory culture and was rather slow-moving.

Phlebotomus carpenteri Fairchild & Hertig

(Plate 25, Fig. e)

First instar larva

Head. Antennal tubercle produced, not prominent. Antenna erect, apical segment several times longer than basal segment. Anterior frontal branched on apical half; posterior frontal short, blunt, branched on apical half; dorsal vertical short, branched throughout length; lateral vertical long, branched on most of length. Thorax and abdomen--Dorsals short, brush-like; lateral setae much longer, conspicuously branched along most of length; caudal setae much longer than body. Two specimens.

See discussion under P. barrettoi.

Phlebotomus cayennensis Floch & Abonnenc

(Plate 6)

Fourth instar larva

Average length 3.5 mm. Ten specimens.

Head. Fronto-vertical region not prominent. Antennal tubercle small, situated directly laternal to anterior frontals. First antennal segment shorter than long; apical segment ovoid, wider than first segment. Integument with spicules slightly curved, arranged in indistinct imbricated design on posterior region.

Thorax and abdomen. Nearly cylindrical. Integument covered with small spicules anteriorly and ventrally, which are replaced dorsally by somewhat larger, more rounded tubercles.

Coloration. Head brown; thorax and abdomen whitish; dorsum of abdominal segment VIII with conspicuous brown patch. Caudal protuberance dark brown.

Chaetotaxy. Head--Posterior frontal, dorsal vertical and lateral ventral brush-like with branches arising nearly throughout lengths, but conspicuous only on distal halves; all of these setae about equal in length, anterior frontal simple, much longer than other cephalic setae. Prothorax--Anterior internal dorsal and laterodorsal equal in length, slightly clavate; anterior external dorsal small, less than half length of internal dorsal; anterior lateroventral not clavate; anterior ventrals acuminate, with sparse, short branches; posterior dorsals unequal in length, internal ones much shorter; posterior external dorsal and posterior lateroventral about one-third length of anterior latero-ventral. Meso- and metathorax--Setae similar to those of posterior row of prothorax, slightly longer. Abdomen--Setae similar to those of metathorax, except dorsals progressively shorter towards posterior end. Internal dorsal of segment VII very short. Intersegmentaries extremely short and inconspicuous. Internal dorsal of segment VIII very short, external dorsal and laterodorsal long; lateroventral simple. Two pairs

of caudal setae present; length 1.8 mm. Internal postanal straight, robust, not whip-like; external postanal long whip-like.

Pupa

Average length 2.2 mm. Two specimens. Respiratory horn directed anteriorly, apex recurved, truncate; pre-alar lobe acute, its setae slightly curved; mesonotal tubercle short, broadly rounded.

Discussion

This is apparently a burrowing species. The antennae are situated anteriorly, the body is cylindrical and pale, and the dorsals are not reduced. Also, the larvae in a laboratory culture showed some burrowing tendencies. It is not obviously closely related to any species of which larvae are known. It may be distinguished by the length of the internal dorsals, which are approximately half as long as the external dorsals, except on the anterior prothorax and eighth abdominal segment. Larvae were not found in nature even though several soil samples from the area where adults were resting were examined. In laboratory cultures they readily fed on sheep feces and insect fragments.

Phlebotomus dasymerus Fairchild & Hertig

(Plate 25, Fig. h)

First instar larva

Head. Antenna with long first segment, as in P. shannoni, situated on prominant, erect tubercle. Posterior frontal and dorsal and lateral verticals long and blunt, with branches only on apical fourth. Two specimens.

Discussion

The structure of the antenna and antennal tubercle would indicate that Fairchild and Hertig (1961) were correct in placing this species near P. shannoni. Gravid females were collected from hollow trees on several occasions, but only a few of the eggs which were deposited ever hatched. The larvae refused to feed on the food available and therefore did not develop past the first instar.

Phlebotomus dysponetus Fairchild & Hertig

While no larvae of this species were reared from identified females, several were recovered from soil samples taken between buttressed roots of trees and reared to the adult stage. No differences were observed between them and larvae of P. camposi.

Phlebotomus galindoi Fairchild & Hertig

(Plate 7)

Fourth instar larva

Average length 4.5 mm. Twenty-five specimens.

Head. Rather short and broad. Antenna situated on very short tubercle, directed anteriorly close to head surface and nearly reaching anterior margin of frons; apical segment narrowed distally, but not pointed; first segment very short, narrower than second. Integument with numerous spicules, posteriorly arranged in an imbricated design.

Thorax and abdomen. Nearly cylindrical. Integument without conspicuous ornamentation.

Coloration. Head brown; thorax and abdomen light tan; dorsum of abdominal segment VIII with brown patch on posterior half, extending laterally to laterodorsal. Caudal protuberance with dorsal surface dark brown, except for anterior margin.

Chaetotaxy. Head--Posterior frontal, dorsal vertical, lateral vertical and anterior frontal brush-like, similar in structure, with branches along entire lengths of setae, these setae rather short; equal to or slightly longer than length of antenna; all other cephalic setae simple. Prothorax--All setae similar in structure and length, except anterior ventrals, which are narrower and more sparsely branched; internal dorsals slightly longer than others in same row. Posterior lateroventral about half length of anterior lateroventral. Meso- and metathorax--Setae similar in structure but much longer than those of prothorax. Abdomen--Setae as in metathorax, almost equal width throughout length, but gradually expanded toward distal ends, with conspicuous transparent bubble-like structure at apex; all dorsals of equal length; intersegmentaries present, long, about two-thirds length of dorsals. Segment VIII with setae as in preceding segments; anterior lateroventral very small. One pair of caudal setae present, length 1.1 mm. Lateral and ventral setae of caudal protuberances long and conspicuous, branched along entire length. External postanal less than twice length of internal anal.

First instar larva

Head. Antenna strongly proclinate, apical segment large, ovoid. Anterior and posterior frontals and dorsal and lateral verticals short, brush-like. Thorax and abdomen--Dorsals rather long, brush-like throughout lengths. Two specimens.

Pupa

Average length 3.2 mm. Three specimens. Respiratory horn and pre-alar lobe inconspicuous; mesonotal tubercle small, shorter than wide.

Discussion

As yet no differences have been found between the larvae of the species of this subgenus (Brumptomyia). Of this group I have reared only P. galindoi from identified females, but large numbers of larvae from natural breeding sites proved to be P. hamatus when reared to the adult stage. Some of these larvae were preserved and show no differences from P. galindoi. Adults of these two species are rarely taken together in nature. P. galindoi was taken from breeding areas on the Atlantic side of the Isthmus and in the higher altitude of Cerro Campana, while P. hamatus was very abundant in the drier regions on the Pacific side of the Isthmus. The larvae are sluggish and readily burrow into food material in laboratory cultures. They were taken from the top few inches of soil between buttressed roots of trees.

Phlebotomus geniculatus Mangabeira

(Plate 8)

Fourth instar larva

Average length 3.6 mm. Three specimens.

Head. Form similar to that of P. panamensis, antennal tubercle large and prominent, well posterior to anterior frontal; first segment of antenna longer than wide; apical segment longer than first segment, direct slightly posteriorly; integument covered with dense spicules, long and curved forward on vertex, not arranged in imbricated design.

Thorax and abdomen. Somewhat depressed. Integument highly ornamented with conspicuous, ridged microtubercles, more pronounced on summits of dorsal swellings.

Coloration. Head brown with distinct whitish dorsal areas which include antennal tubercles and extend posteriorly and ventrally to include lateral vertical setae. Thorax and abdomen light tan with light brown dorsal patches arranged to form interrupted stripe on each side. Segment VIII of abdomen with brown dorsal patch; caudal protuberance brown dorsally.

Chaetotaxy. Head--Posterior frontals long and attenuate, with only few inconspicuous short branches; dorsal verticals shorter, more conspicuously branched; all other cephalic setae simple. Prothorax--Only one pair of anterior dorsals present, slightly branched on distal half; anterior lateroventral directed, ventrad, with microseta anterior to it. Posterior dorsals clavate, branched, about equal in length to anterior dorsals; anterior lateroventral branched throughout its length; posterior lateroventral shorter, branched only at distal end; external ventral branched only on distal half; internal ventral simple. Meso- and metathorax--Dorsals short, directed caudad, branched at apices; anterior and posterior laterodorsals close together, with long, narrow branches throughout most of length; other setae as on prothorax. Abdomen--Setae as on metathorax except for ventrals; intersegmentaries present, similar to dorsals. Segment VIII with internal dorsals very short and knob-like; external dorsals long, situated posterior to spiracles; laterodorsal conspicuously branched, the branches long and narrow; lateroventral directly anterior to laterodorsal and about half its length, situated with brown dorsal patch. T o pairs of caudal setae present, length 2.5 mm; lateral seta of protuberance branched on distal half, blunt; ventral seta simple, longer. Internal postanal short, subappressed; external postanal rather long.

Discussion

This species is easily recognized by the conspicuous pale areas of the otherwise brown head capsule, and by the markings of the thorax and abdomen, which give it a striped effect. Otherwise it is similar in form to P. panamensis. The larvae are well camouflaged while feeding upon dead leaves in laboratory cultures, as they are similarly colored. They remain motionless for long periods of time and move only when seeking food.

Phlebotomus gomezi Nitzulescu

(Plate 9)

Fourth instar larva

Average length 3.6 mm. Three specimens.

Head. Fronto-vertical profile not evenly curved, frons more prominent than vertex; antenna situated on rather short tubercle, well posterior to anterior frontal; antenna erect, first segment short, apical segment bent backward at its middle, not expanded. Integument covered with rather evenly distributed spicules, no imbricated design evident, but a few curved rows present.

Thorax and abdomen. Somewhat cylindrical. Integument covered with inconspicuous, blunt spicules.

Coloration. Head light brown, thorax and abdomen creamy white, abdomen with light brown patch on dorsum of segment VIII, caudal protuberance brown.

Chaetotaxy. Head--Anterior frontal and lateral vertical simple; posterior frontal and dorsal vertical branched throughout their lengths, erect, strongly curved forward; dorsal verticals posterior to posterior

frontals. Prothorax--Anterior dorsals, anterior laterodorsal and anterior lateroventral similar, conspicuously branched only on their distal halves; anterior external dorsal slightly shorter than internal dorsal; posterior dorsals similar to anterior dorsals, but internal dorsals directed backward and external dorsals strongly forward; posterior lateroventral rather short; posterior ventrals branched as in dorsals. Meso- and metathorax--Setae as on posterior prothorax, except anterior and posterior lateroventrals close together. Abdomen: Segments I-VII--Setae as on metathorax, except posterior lateroventral simple and much more ventral than anterior lateroventral; segment VIII with internal dorsal as on previous segments; external dorsal long, extending past caudal protuberance, branched on distal two-thirds; lateroventral reduced to size of micro-seta. Two pairs of caudal setae present, length 2.0 mm; internal postanal directed ventrad, external postanal very long, whip-like.

First instar larva (fig. f)

Head. Antenna erect, on short tubercle, apical segment much longer than basal segment, not curved. All setae simple. Thorax and abdomen--Setae relatively long, only slightly branched at distal ends. Caudal setae much longer than body. Two specimens.

Pupa

Average length 2.7 mm. Eight specimens. Respiratory horn blunt, parallel sided; pre-alar setae strong; mesonotal tubercle long, curved posteriorly; mesonotum strongly produced along median line. Dorsal tubercles of abdomen prominent.

Discussion

Although this species is a surface-feeder, at least in laboratory cultures, it shows few characters which would place it with group 2. It shows an affinity with P. vexillarius in that the external dorsals are directed strongly forward in contrast to the other dorsals, which are directed backward. P. gomezi has a distinctly paler head capsule, and the internal dorsal of abdominal segment VIII is longer, about one-half the length of the external dorsal. It is more active than most species and seems to favor certain molds as food in laboratory cultures. It was not recovered from natural habitats even though areas where adults were abundant were intensively searched.

Phlebotomus hansoni Fairchild & Hertig

(Plate 25, Figs. a - d)

Although this species was reared to the adult stage from wild-caught larvae, none of the larvae were preserved, and only the pupal cases with their attached larval skins remain. Most of the setae are attached but difficult to identify because of the contorted skin. However, the identifiable characters are as follows:

Head brown, antenna small, first segment shorter than apical segment, situated anteriorly, near level of anterior frontal setae. All dorsal cephalic setae short, brush-like. Integument of head capsule with distinct imbricated design posteriorly. Setae of thorax brush-like throughout their lengths, dorsals about equal in length. Setae of posterior abdominal segments long, clavate; all dorsals about equal in length except internal dorsals of eighth segment, which are short, less than one-fourth length of external dorsal. Two pairs of caudal setae present.

The larvae were recovered from soil samples taken from the areas between buttressed roots of trees on the Atlantic side of the Canal Zone. They were reared on regular Phlebotomus food without difficulty. It was not observed whether or not they borrowed into the food material of feces and dead leaves.

Phlebotomus hartmanni Fairchild & Hertig

(Plate 10)

All stages like those of P. sanguinarius except for the following characters of the fourth instar larva: Anterior external dorsal of prothorax distinctly less than one-half length of anterior internal dorsal. Posterior prothorax, meso- and metathorax with internal dorsals extremely short. Three specimens.

Discussion

The larvae of P. hartmanni are very similar to those of P. sanguinarius in structure as well as habits; however, in the latter species the anterior external dorsal of the prothorax is more than half the length of the anterior internal dorsal, and the internal dorsals of the posterior prothorax and the other segments of the thorax and abdomen are longer than those of P. hartmanni. Adults of this species are not often collected, but it was one of the few species taken in the cloud forest of Cerro Campana. It was reared without difficulty in the laboratory under the same conditions as P. sanguinarius.

Phlebotomus ovallesi Ortiz

(Plate 11)

Fourth instar larva

Average length 3.1 mm. Four specimens.

Head. Fronto-vertical region somewhat flattened. Antennal tubercle very small, well forward on head, at level of anterior frontal. Antenna directed anteriorly; first antennal segment very small, apical segment wider, ovoid. Integument with slender, slightly curved microtrichia, posteriorly arranged in imbricated design; anterior region of head capsule bare.

Thorax and abdomen. Somewhat cylindrical. Integument covered with spicules, which are in form of tubercles with pointed apices on summits of dorsal swellings.

Coloration. Head brown, thorax and abdomen whitish with brown patch on dorsum of abdominal segment VIII. Caudal protuberances dark brown.

Chaetotaxy. Head--Anterior frontal sparsely branched; posterior frontal, lateral vertical and dorsal vertical brush-like, distinctly clavate, not acute at apices. Posterior frontal closer to vertex than is dorsal vertical, as seen in lateral aspect. Prothorax--Anterior row of internal dorsal, laterodorsal and lateroventral about equal in length and brush-like; external dorsal less than one-half length of internal dorsal. Ventrals brush-like, not acuminate. Posterior internal dorsal much shorter than posterior external dorsal. Posterior lateroventral very short. Meso- and metathorax--Setae like those of posterior prothorax, except that internal dorsal at least as long as external dorsal. Abdomen--Setae as on metathorax, except that

internal dorsals very short. Intersegmentaries extremely small. Internal dorsal of segment VIII very small; external dorsal long and brush-like, arising well posterior to spiracle; laterodorsal well developed; lateroventral present only as microseta. Two pairs of caudal setae present, length 1.3 mm. External postanal nearly twice length of internal postanal.

Pupa

Length 2.4 mm. One specimen. Respiratory horn and prealar lobe prominent; mesonotal tubercle broad, directed somewhat anteriorly. Mesonotum with distinct depression anterior to mesonotal tubercle. Abdomen without prominent dorsal tubercles.

Discussion

This species is similar in size and overall appearance to P. serranus and P. trinidedensis, but the lengths of various dorsal setae differ greatly among these species. In P. ovallesi the internal dorsals of the abdominal segments are very short, while the external dorsal of segment VIII is long. Also, the dorsal vertical of the head is situated posterior to the lateral vertical. This species shows burrowing tendencies in laboratory cultures and has been recovered several times from soil samples between buttressed roots of trees.

Phlebotomus panamensis Shannon

(Plate 12)

Fourth instar larva

Average length 3.5 mm. Two specimens.

Head. Frontal area prominent, frontovertical angle, as seen in lateral aspect approaching 90°. Gular region strongly inflected. Antennal tubercle as long as antenna, situated well posterior to anterior frontals. Basal and apical antennal segments about equal in length; apical segment directed dorsad at slight angle from basal segment, slightly wider. Mandible with upper margin straight through most of its length, the apex strongly curved. Clypeus undulate in profile, protruding at origins of both anterior and posterior clypeal setae.

Thorax and abdomen. Flattened dorso-ventrally. Integument conspicuously covered with numerous minute wart-like tubercles. Prominent lateral protuberances bear the lateral setae.

Coloration. Head pale gray except for mandibles, which are black, and clypeus, which is brown; thorax and abdomen uniformly grayish. Only apices of caudal protuberances dark brown or black.

Chaetotaxy. Head--All setae similar in structure, slightly curved anteriorly, darker than head integument, appearing simple, but posterior setae possess minute sparse branches as seen under high magnification; dorsal vertical caudad to and much shorter than posterior frontal. Prothorax--Anterior dorsals proclinate, only one pair present, produced on conspicuous tubercles about one-half length of setae; anterior laterodorsal similar to and same length as anterior dorsals; anterior lateroventral strong, directed slightly cephalad, curved downward at apex, located directly anterior to spiracle; posterior dorsals short, erect, curved slightly caudad; anterior ventrals simple, posterior ventrals with short branches. Meso- and Metathorax--Dorsals equal in length to those of prothorax, directed more caudad; laterodorsal much longer than dorsals; anterior lateroventral as in prothorax, posterior lateroventral present, on a conspicuous swelling, but directed slightly

caudad; ventrals similar to those of prothorax, but slightly longer. Abdomen--Dorsals similar to those of metathorax; laterdorsal long, rather straight, directed caudad; anterior and posterior lateroventrals on separate swellings, similar, directed somewhat ventrad. Intersegmentaries about half length of dorsals. Segment VIII: Dorsals very minute and inconspicuous, appearing only as small knobs; laterodorsal and posterior lateroventral long; anterior lateroventral much shorter and more slender. Two pairs of caudal setae present, length 3.0 mm. Internal postanal inconspicuous, short, directed ventrad; external postanal rather long, extending well past anal protuberance.

First instar larva

Head. Antenna erect, on prominent, narrow, erect tubercle nearly as long as antenna. Setae simple, posterior frontal longest. Six specimens.

Pupa

Length approximately 3.2 mm. One specimen. Respiratory horn and prealar lobe prominent; mesonotal tubercle long; mesonotum strongly keeled. Wing sheaths noticeably slender. Abdomen without tubercles. Color dark gray.

Discussion

The fourth instar larva of this species has a dark gray thorax and abdomen and a pale gray head, which give it a distinctive appearance. The only other species with this combination of characters is P. pessoana, from which it can hardly be distinguished. It also has ear-like antennal tubercles and a conspicuously flattened body. In general appearances it resembles P. apicalis, but in that species the head is distinctly

globular, the prothorax is pale gray, and there are two pairs of anterior prothoracic dorsals. P. panamensis has only one pair of dorsals in the anterior row of the prothorax. This species is strictly surface feeding and was found in nature several times on moist, dead leaves on the soil surface. On such a background the larva is well comouflaged. As in other surface feeders, the larvae usually remain motionless until disturbed, at which time the long, vertical caudal setae are jerked slightly forward at intervals. Pupation takes place on the upper side of dry leaves, where the pupa is also protectively colored. Rearing in the laboratory of this common man-biting species has proved difficult, and only a small percentage of the larvae survived to the adult stage.

Phlebotomus pessoana Barretto

(Plate 12, Fig. h)

Six specimens. This species is very close to P. panamensis, and the immature stages are almost indistinguishable. The only character found to differ is the size of the anterior prothoracic dorsal setae. In P. pessoana they are weaker and shorter than those of P. panamensis, and the inner pair are about half as long as the outer (laterodorsals). In P. panamensis the inner pair are about two-thirds as long as the outer. However, this difference is slight and may not be significant.

The two species have similar habits, but P. pessoana is even more difficult to rear and seems to require slightly cooler temperatures. Larvae were recivered from decaying leaves on the soil surface in thick forest in the same area where resting adults were numerous.

Phlebotomus pinealis Floch & Abonnenc

(Plate 25, Fig. g)

First instar larva

Head. Antenna situated at approximate level of anterior frontals, somewhat proclinate. Apical segment ovoid, much broader than basal segment. Anterior and posterior frontals and dorsal and lateral verticals equal in length, branched throughout lengths. Thorax and abdomen--Setae conspicuously branched throughout lengths. Two specimens.

Discussion

The larvae would not feed on the food available and thus could not be reared past the first instar. The anterior position of the antennae and short brush-like head setae indicate that it is probably a burrower. Its relationship to other species based on larval characters is uncertain, but there appears to be little evidence to support Fairchild's placing it with P. vespertilionis.

Phlebotomus rubidulus Fairchild & Hertig

(Plate 13)

Fourth instar larva

Average length 2.7 mm. Three specimens.

Head. Fronto-vertical region somewhat flat, not produced; antennal tubercle small, situated slightly anterior to anterior frontal seta. Antenna directed forward; first segment small, shorter than wide; apical segment ovoid, much wider and longer than first segment. Integument covered with short spicules, strongly curved forward, posteriorly arranged in curved lines, giving an imbricated effect.

Thorax and abdomen. Generally cylindrical. Integument covered with spicules, dorsally developed into pointed tubercles.

Coloration. Head brown, with dorsal oral margin darker. Thorax and abdomen whitish, segment VIII with dorsal brown patch; caudal protuberance dark brown.

Chaetotaxy. Head--Anterior and posterior frontals and lateral and dorsal verticals similar in length and structure: all brush-like, with branches covering at least distal half, longest near apices of setae. Dorsal vertical posterior to lateral vertical as seen in lateral aspect. Prothorax--Anterior internal dorsal, anterior laterodorsal and anterior lateroventral similar, clavate and brush-like on distal half. Anterior external dorsal very small, about one-fourth length of internal dorsal. Posterior internal dorsal short and expanded distally. Posterior external dorsal and posterior laterodorsal long, clavate and brush-like distally. Posterior lateroventral very short, knob-like. Meso- and metathorax--Setae similar to those of posterior prothorax, but external dorsals slightly longer. Ventrals clavate and conspicuously brush-like. Abdomen--Segments I to III with external dorsals much longer than internal dorsals; on segments IV to VII external dorsals nearly as short as internal dorsals. Laterodorsals on segments VI and VII smaller than those of previous segments; anterior lateroventral long: posterior lateroventral small, knob-like on each segment. Intersegmentaries very small. Segment VIII with internal and external dorsals small, equal in length, both in a transverse line with spiracle. Laterodorsal long, brush-like on distal half. Lateroventral microsetiform. Two pairs of caudal setae present, length

1.8 mm. External postanal not especially long, no more than twice length of internal postanal.

Pupa

Average length 2.0 mm. One specimen. Respiratory horn and prealar lobe prominent; mesonotal tubercle large, directed somewhat forward; mesonotum with strong identation anterior to it. Abdomen with well developed dorsal tubercles curved posteriorly.

Discussion

In the larvae of this small species the body setae are conspicuously clavate, more so than in any other species examined. The internal dorsals of the thorax and abdomen and the external dorsals of abdominal segments VII and VIII are extremely short, a condition seen only in P. sanguinarius and P. hartmanni. However, these share few other characters with P. rubidulus. Fairchild (1957) placed this species in the anthophorus group based on adult characters. The only other species in that group of which larvae have been described is P. anthophorus, which Addis (1945) shows as having long external dorsals on abdominal segment VIII. This species was rather easily reared in the laboratory. Gravid females were taken during the dry season from dead leaves at Cerro Galera.

Phlebotomus runoides Fairchild & Hertig

(Plate 14)

Fourth instar larva

Average length 3.0 mm. Two specimens.

Segments I to VII with external dorsals small, about equal to internal dorsal; laterodorsals progressively smaller toward posterior end, on segment VII about twice as long as dorsals; lateroventrals about same length on each segment. Intersegmentaries very small. Segment VIII with internal dorsal very samll, external dorsals much longer, considerably posterior to spiracle; laterodorsal long; lateroventral only a small, simple seta, directly below microseta. Two pairs of caudal setae present, length 2.5 mm. Internal postanal not appressed as in most other species; external postanal long and whip-like.

First instar larva

Head. Antennal tubercle prominent, not directed backward. Apical segment of antenna longer than tubercle, gently curved backward. Dorsal vertical and lateral vertical straight, stout, brush-like only at extreme apices. Two specimens.

Discussion

This species possesses the following distinctive characters in the larval stage: The distal segment of the antenna is strongly curved posteriorly, all dorsal setae are short, especially on the abdomen, and the external dorsals of the thorax are strongly clavate. In the upward directed antennal tubercle and general shape of the head, this species resembles P. shannoni, although the first antennal segment is very short, whereas in P. shannoni it is longer than the distal segment.

Phlebotomus sanguinarius Fairchild & Hertig

(Plate 15)

Fourth instar larva

Length 4.1 mm. Eight specimens.

Head. Comparatively large, about twice as long as wide as seen in lateral aspect; mandibles and hypostome thick, robust; antennal tubercle absent or only slightly developed; antenna small, directed forward from head at approximate level of anterior frontal; first segment short and inconspicuous, apical segment wider, ovoid; integument with spicules on posterior half, arranged in imbricated design, with narrow anterior extensions to antennae and lateral verticals, and a ventral extension on hypostomal bridge.

Thorax and abdomen. Rather cylindrical. Integument not conspicuously ornamented, covered with small, pointed tubercles, some of them on dorsum strongly curved.

Coloration. Head dark brown; thorax and abdomen whitish, with brown patch on dorsum of segment VIII of abdomen; caudal protuberance darkly pigmented.

Chaetotaxy. Head--Setae long and slender; posterior frontal and dorsal vertical with only short branches on distal half, other setae simple. Prothorax--Anterior internal dorsal and laterodorsal long, sparsely branched on basal three-fourths, brush-like on distal fourth; anterior external dorsal brush-like on apical third, length less than one-half length of internal dorsal; anterior lateroventral narrowly brush-like on apical half; anterior ventrals with short branches only on apical fourth; posterior internal dorsal very short, knob-like; posterior external dorsal and posterior laterdorsal long and brush-like

on distal third; posterior lateroventral small, about one-fourth length of anterior lateroventral; posterior ventrals narrowly brush-like on distal half. Meso- and metathorax--Setae approximately as in posterior prothorax, except anterior and posterior lateroventrals close together. Abdomen--All internal dorsals very short, as in mesothorax; external dorsals progressively shorter towards posterior end, variable on segment VII, very short on segment VIII; lateroventrals long on all segments. Intersegmentaries extremely small. Caudal setae rather short, internal pair 1.8 mm. Both internal and external postanals long, curved downward.

First instar larva

Head. Mandible strong, recurved at apex. Antenna nearly erect, apical segment segment large, much wider than basal segment. Setae simple. Thorax and abdomen. Coloration pale. Setae with short branches at apex. One specimen.

Pupa

Average length 3.2 mm. Five specimens. Respiratory horn relatively long; pre-alar lobe short; mesonatal tubercle prominent, slightly curved backward; dorsal abdominal tubercles strongly developed, directed posteriorly.

Discussion

All stages nearly identical to those of P. hartmanni, and the differences are pointed out in the discussion of that species. These two species are easily distinguished from others by the relatively large, nearly black, shiny head. The antenna is conspicuously small and

directed forward. The head and trunk setae are not conspicuously brush-like, but are slender and appear dark against the pale thorax and abdomen. P. sanguinarius is a sluggish species and readily crawls under the food material in laboratory cultures, where it is easily reared. Despite considerable searching in areas where adults were numerous, no larvae were found in natural habitats. This is one of the commonest man-biting species in Panama.

Phlebotomus serranus Damasceno & Arouck

(Plate 16)

Fourth instar larva

Average length 3.3 mm. Four specimens.

Head. Fronto-vertical region somewhat flattened, not produced. Antennal tubercle very short and inconspicuous. Antenna situated well forward, lateral to anterior frontal, directed anteriorly; first antennal segment almost as long as wide, narrower than apical segment, which is ovoid. Integument with slender, erect microtrichia conspicuously arranged in imbricated design posteriorly; anterior region of head capsule bare.

Thorax and abdomen. Somewhat cylindrical. Integument covered with spicules, which form tubercles with pointed apices on summits of dorsal swellings.

Coloration. Head brown, thorax and abdomen whitish with brown patch on dorsum of abdominal segment VIII caudal protuberance brown.

Chaetotaxy. Head--Anterior frontal acuminate, sparsely branched; posterior frontal, lateral vertical and dorsal vertical brush-like, widest in middle, somewhat acute at apices; dorsal vertical close to vertex than is posterior frontal as seen in lateral aspect. Prothorax--Anterior row

of internal dorsal, laterodorsal and lateroventral equal in length, brush-like; external dorsal more than one-half length, of internal dorsal; ventrals acuminate, sparsely branched. Posterior internal dorsal long, about equal to external dorsal of same row; posterior lateroventral short, about one-fourth length of anterior lateroventral. Meso- and metathorax--Setae like those of posterior prothorax. Abdomen--Setae much the same as those of metathorax; anterior lateroventral long on each segment; posterior lateroventral somewhat shorter, brush-like. Intersegmentaries prominent. Internal dorsal of segment VIII short but not extremely so; external dorsal long, arising only slightly posterior to spiracle; laterodorsal long, about equal in length to external dorsal; lateroventral well developed, more than one-half length of laterodorsal. Two pairs of caudal setae present, length 1.4 mm. Internal postanal stout, strongly curved; external postanal whip-like, but not particularly long.

Pupa

Average length 2.4 mm. Two specimens. Respiratory horn and prealar tubercle prominent; mesonotal tubercle rather short, obtuse. Abdomen with well developed dorsal tubercles.

Discussion

In this species all of the dorsal setae are long and erect, with the exception of the internal dorsal of abdominal segment VIII, which is very short. These setae are conspicuously brush-like on the distal two-thirds. P. serranus was easily reared in the laboratory and was recovered several times from soil samples taken between buttressed roots of trees. On one occasion several larvae were discovered feeding on a dead caterpillar.

Phlebotomus shannoni Dyar

(Plate 17)

Fourth instar larva

Average length 3.3 mm. Five specimens.

Head. Rather large, vertex prominent. Antennal tubercle long, conspicuously aboral, longer than antenna. Antenna slender, first segment longer than wide and longer than second, the latter directed backward at slight angle from first segment. Integument covered with numerous spicules, arranged into imbricated design posteriorly.

Thorax and abdomen. Somewhat flattened dorso-ventrally, rather short and broad. Integument covered with spicules, which on summits of dorsal swellings grade into rounded tubercles.

Coloration. Head brown, thorax and abdomen light tan, with dorsal brown patch on abdominal segment VIII. Caudal protuberance dark brown.

Chaetotaxy. Head--All setae simple except for few sparse microscopic branches on frontals and verticals; setae very long. Prothorax--Two pairs of anterior dorsals present, rather short, sparsely branched on distal two-thirds; anterior lateroventral much longer, acuminate, and sparsely branched nearly to base. Posterior dorsals smaller than anterior dorsals, erect. All other setae similar in structure, slender, sparsely branched. Meso- and metathorax--Setae similar to those of posterior prothorax, but reclinate. Abdomen--Dorsals shorter than those of thorax. Laterdorsals and lateroventrals long, acuminate, the former reclinate, the latter declinate. Intersegmentaries very small. Internal dorsal of segment VIII very short, external dorsal several times longer; lateroventral more than half length of laterodorsal. Two pairs of

caudal setae present, length 3.1 mm. Internal postanal reclinate, long; external postanal very long and whip-like. Lateroanal slender, longer than internal postanal.

First instar larva

Head. Antennal tubercle prominent, directed strongly backward. Antenna straight, directed backward; basal segment equal in length to apical segment. Anterior frontal long, only slightly branched; posterior frontal, dorsal vertical and lateral vertical blunt, slightly branched at apices. Thorax and abdomen--Anterior internal dorsal of prothorax at least three times as long as posterior internal dorsal, which is expanded distally. Two specimens.

Pupa

Average length 2.7 mm. Five specimens. Respiratory horn prominent. Prealar lobe rather long, two apical setae slightly curved. Mesonotal tubercle moderately long, directed away from head. Abdomen without dorsal tubercles.

Discussion

In overall appearance the fourth instar resembles that of P. trapidoi but is more robust, and the antennae and antennal tubercles are distinctive in being strongly directed toward vertex of head. Two pairs of dorsals are present in the anterior row of prothoracic setae. It is surface-feeding and sluggish; the long, caudal setae are held upright. It was never recovered from soil samples, and its natural habitat is unknown. However, it likely inhabits decaying leaves on the forest floor. This species was easily reared in the laboratory, feeding on feces, dead insects and leaf fragments.

Phlebotomus spinosus Floch & Abonnenc

(Plate 18)

Fourth instar larva

Average length 3.1 mm. Five specimens.

Head. Rather large, profile of fronto-vertical region evenly curved as seen in lateral aspect. Antennal tubercle somewhat produced, about equal in length to setal tubercles but much wider, situated slightly posterior to anterior frontal seta. Antenna erect, first segment short, wider than long; apical segment slightly bent posteriorly at middle. Integument thickly covered with spicules, which are strongly curved forward, vaguely arranged in imbricated design posteriorly.

Thorax and abdomen. Rather cylindrical. Integument thickly covered with minute spicules ventrally, grading into rounded tubercles dorsally.

Coloration. Head brown, thorax and abdomen pale tan, with dorsal light brown patch on abdominal segment VIII.

Chaetotaxy. Head--All setae long and acuminate, frontals and verticals sparsely branched on distal two-thirds. Prothorax--Anterior internal dorsal, anterior laterodorsal and anterior lateroventral long and slender, sparsely branched on distal two-thirds; anterior external dorsal small, less than half length of internal dorsal. Posterior internal dorsal shorter than posterior external dorsal; posterior laterodorsal similar to anterior laterodorsal; posterior lateroventral short. Meso- and metathorax--Setae similar to those of posterior prothorax, but longer. Abdomen--Dorsals progressively shorter posteriorly, very short on segment eight. Laterodorsals long throughout body length. Anterior lateroventral about one-third shorter than

laterodorsal; posterior lateroventral slightly shorter than anterior lateroventral. Intersegmentaries very small, difficult to see. Internal dorsal of eighth segment very small, external dorsal and laterodorsal much longer, about equal in length, branched as in other long setae. Lateroventral very short and inconspicuous. Two pairs of caudal setae present, length 2.0 mm. Internal and external postanals very long, whip-like, nearly equal in length.

Pupa

Length 2.3 mm. Four specimens. Respiratory horn prominent, long. Prealar lobe short, with two apical setae. Mesonotal tubercle rather short, posterior to deep notch. Abdomen without conspicuous dorsal tubercles.

Discussion

This uncommon species does not show any obvious relationship with any known species and is thus difficult to place. The antennae are erect, but the body is not flattened. It was not noted to burrow in laboratory cultures. It appeared to be mainly surface feeding.

Phlebotomus trapidoi Fairchild & Hertig

(Plate 19)

Fourth instar larva

Average length 3.0 mm. Four specimens.

Head. Fronto-vertical profile rather evenly rounded, as seen in lateral aspect. Antennal tubercle large, situated about midway between anterior and posterior frontal setae, as seen in lateral aspect. First

segment of antenna much longer than wide, but shorter than apical segment, which is rather narrow, bent slightly at middle. Integument covered with conspicuous spicules curved forward. Setal tubercles prominent.

Thorax and abdomen. Somewhat flattened dorso-ventrally. Integument with minute spicules, less conspicuous than those of P. panamensis.

Coloration. Head brown, thorax and abdomen pale tan, with dark brown patch on dorsum of abdominal segment VIII, bordered by laterodorsals, lateroventrals and dorsals; caudal protuberance dark brown.

Chaetotaxy. Head--Posterior frontal, dorsal vertical and lateral vertical with short branches on distal half only; posterior frontal strongly curved forward near apex; anterior frontal simple except for sparse, minute branches. Prothorax--Only one pair of anterior dorsals present; anterior laterodorsal nearly twice length of anterior dorsal, both branched only on apical half; one microseta present below laterodorsal; anterior ventrals with only short, sparse branches on distal half. Posterior internal dorsal very short, expanded and rosette-like with branches rounded apically; posterior external dorsal slightly longer but similar, the branches narrower; posterior laterodorsal longer, with branches as in other setae; posterior lateroventral extremely short, knob-like. Meso- and metathorax--Setae as on posterior prothorax, except anterior and posterior lateroventrals approximate and on same tubercle. Abdomen--Dorsals, laterodorsal and anterior lateroventrals as on mesothorax; posterior lateroventral situated much below anterior lateroventral, directly dorsad from ventral seta, about half length of anterior laterodorsal. Intersegmentaries extremely small and inconspicuous. Internal dorsal of segment VIII small, knob-like,

external dorsal and laterodorsal long, sparsely branched on distal half, the branches subappressed; lateroventral about one-third length of laterodorsal, slightly clavate, branched at apex. Two pairs of caudal setae present, length 2.4 mm. Internal postanal subappressed; external postanal long, whip-like.

First instar larva

Head. Antennal tubercle prominent. Antenna erect, apical segment longer than basal segment. Setae simple. Four specimens.

Pupa

Average length 2.1 mm. Three specimens. Respiratory horn long; prealar lobe directed forward, with two slightly curved apical spines; mesonotal tubercle prominent, directed somewhat forward. Abdomen with dorsal tubercles only slightly produced.

Discussion

A surface feeder, this species is rather slow-moving and inconspicuous on the decaying leaves upon which it feeds. Larvae were found on a few occasions on moist, dead leaves a few feet from a tree trunk where many adults were often collected. The antennal tubercles are enlarged and the dorsal head setae are quite strongly curved. The body is somewhat flattened, but less so than that of P. panamensis. While it has been reared in the laboratory on several occasions, it does not thrive there, partly because of mold, which interferes with especially the early stages. The adults readily feed on man.

Phlebotomus trinidadensis Newstead

(Plate 20)

Fourth instar larva

Average length 3.2 mm. Five specimens.

Head. Fronto-vertical region not prominent. Antennal tubercle short, inconspicuous, situated about even with anterior frontal. Antenna directed forward; first segment very short, much wider than long; apical segment broadly ovate, wider than first segment. Integument with spicules curved forward, almost all arranged in curved rows, giving a conspicuous imbricated effect over most of dorsal and lateral regions.

Thorax and abdomen. Rather cylindrical. Integument covered with spicules, which on dorsum grade into broadly rounded tubercles.

Coloration. Head brown, thorax and abdomen whitish, with brown patch on dorsum of eighth abdominal segment; caudal protuberance dark brown.

Chaetotaxy. Head--Anterior and posterior frontals and dorsal and lateral verticals brush-like, about equal in length; dorsal verticals distinctly clavate. Prothorax--Anterior internal dorsal clavate, much longer than external dorsals, the latter very short; anterior laterodorsal and anterior lateroventral about equal in length and brush-like; anterior ventrals slender, weakly branched. Posterior internal dorsal very short, less than one-fourth length of posterior external dorsal; posterior laterodorsal long, clavate; posterior lateroventral very small and knob-like. Meso- and metathorax--Setae as on posterior prothorax, but external dorsal longer. Abdomen--Setae as on metathorax except that external dorsals become progressively shorter toward posterior end; external dorsal of segment V less than

half length of same on segment I. Intersegmentaries very small. External dorsal of segment VIII same length as internal dorsal and intersegmentaries; both dorsals of segment VIII very short, dorsolateral long. Two pairs of caudal setae present, length 1.0 mm. Internal postanal slightly decurved, external postanal whip-like, not especially long.

Pupa

Average length 2.6 mm. Five specimens. Respiratory horn prominent. Prealar lobe acute, directed forward; two apical setae long, slightly curved. Mesonotal tubercle shorter than wide, directed away from head. Abdomen with prominent dorsal tubercles.

Discussion

Although P. trinidadensis is the most frequently encountered species in Panama, the larvae were recovered on only a few occasions from soil samples. They readily burrow into the food material in laboratory cultures and thus undoubtedly burrow in the soil in natural habitats. This wpecies was easily reared in the laboratory. The very short internal dorsal of the mesothorax, in contrast to the much longer external dorsal, distinguishes this species from all others except P. sanguinarius, P. hartmanni, and P. rubidulus. From the former two it is distinguished by the much smaller head and more brush-like setae, and from the latter by the relative positions of the dorsal and lateral verticals of the head. In P. rubidulus, as in P. ovallesi, the dorsal vertical is posterior to the lateral vertical, while in P. trinidadensis the lateral vertical is posterior. In Fairchild's classification P. trinidadensis is placed along with P. sanguinarius and P. hartmanni in the vexator group. There are few larval characters which will support this grouping. They are alike in possessing very

short external dorsals of abdominal segment VIII, but in a Brazilian species, P. oswaldoi, also of this group, these setae are long. P. rubidulus of the anthophorus group also has short external dorsals. (In P. anthophorus, however, they are long.)

Phlebotomus triramulus Fairchild & Hertig

(Plate 21)

Fourth instar larva

Average length 3.5 mm. Five specimens.

Head. Fronto-vertical region not prominent. Antennal tubercle small, situated slightly anterior to anterior frontal setae. Antenna directed forward; first segment short; apical segment ovoid, wider and much longer than first segment. Integument covered with long, slender and slightly curved spicules, conspicuously arranged in imbricated design posteriorly.

Thorax and abdomen. Rather cylindrical. Integument covered with spicules, supplanted on summits of dorsal swellings by rounded or pointed tubercles.

Coloration. Head brown, thorax and abdomen whitish, with brown patch on dorsum of abdominal segment VIII; caudal protuberance dark brown.

Chaetotaxy. Head--Anterior frontal attenuate, only sparsely and minutely branched; posterior frontal, dorsal vertical, and lateral vertical brush-like, not attenuate, about equal in length. Prothorax--Anterior internal dorsal, anterior laterodorsal and anterior latero-ventral rather long, apical four-fifths brush-like, branches longer at

apices; anterior external dorsal much shorter, about half length of anterior internal dorsal. Posterior external dorsal unusually long, about twice length of internal dorsal; posterior laterodorsal as on anterior prothorax; posterior lateroventral small, about one-fourth length of anterior lateroventral; ventrals brush-like. Meso- and metathorax--Internal dorsals very long, longer than external dorsal. Other setae similar to those of posterior prothorax. Abdomen--Internal dorsals very long on segments I-VI, very short on segment VII; external dorsals long throughout; laterodorsals very long, nearly twice length of anterior lateroventrals; posterior lateroventrals reduced to microsetae. Internal dorsal of segment VIII short, as on segment VII; external dorsal very long; laterodorsal somewhat shorter; lateroventral about equal to length of anterior lateroventral of preceeding segment. Two pairs of caudal setae present, length 1.2 mm. External postanal whip-like, not especially long, but at least twice length of internal postanal.

First instar larva

Head. Clypeus very prominent. Antenna proclinate, apical segment large, ovoid. Anterior frontal long, blunt, branched only at extreme apex; posterior frontal, dorsal vertical and lateral vertical much shorter, brush-like throughout lengths. Anterior prothoracic dorsal long, brush-like on apical half; remaining dorsals much shorter. Two specimens.

Pupa

Length 2.3 mm. Four specimens. Respiratory horn not prominent. Prealar lobe long and conspicuous, with two apical spines of equal

length. Mesonotal tubercle curved backward, posterior to rather deep notch. Abdomen with large dorsal tubercles.

Discussion

This species was easily reared in the laboratory, where it showed burrowing tendencies. It possesses distinctive long dorsals in the fourth instar, but these are considerably shorter and straighter than those of P. longispinus Mang., a closely related Brazilian species. Like that species, P. triramulus possesses very short internal dorsals of the abdominal segments VII and VIII contrasting with the extremely long setae of the preceding segments.

Phlebotomus vespertilionis Fairchild & Hertig

(Plate 22)

Fourth instar larva

Average length 4.0 mm. Three specimens.

Head. Large, ovoid. Antenna erect, arising from short tubercle situated slightly posterior to anterior frontal setae; first segment longer than wide, apical segment wider and one-third longer than first segment, bent slightly backward at apex. Integument with minute spicules rather sparsely distributed over posterior region, conspicuously arranged in imbricated design.

Thorax and abdomen. Cylindrical and rather slender. Integument covered with spicules, dorsally much thicker and more prominent, apices pointed.

Coloration. Head light brown, thorax and abdomen whitish, with small, light brown patch on dorsum of eighth abdominal segment; caudal protuberance brown.

Chaetotaxy. Head--Posterior frontal and dorsal vertical sparsely branched on distal half; other setae simple. Prothorax--Anterior internal dorsal long, brush-like on distal half; anterior external dorsal very small, not more than one-fourth length of internal dorsal; anterior laterodorsal and anterior lateroventral same length and appearance as internal dorsal. Posterior external dorsal and laterodorsal long and brush-like; posterior lateroventral very small. Meso- and metathorax--Setae similar to those of posterior prothorax. Abdomen--Dorsals progressively shorter toward posterior end, very short on segment VII; laterodorsals and lateroventrals of uniform length throughout; anterior lateroventrals longer and more slender than laterodorsals; posterior lateroventrals less than half length of anterior lateroventral; all setae branched on distal half. Internal dorsal of segment VIII very short, external dorsal and laterodorsal several times longer; lateroventral reduced to simple microseta. Two pairs of caudal setae present, length 2.0 mm. Internal postanal slightly curved, not whip-like; external postanal long, whip-like.

Pupa

Length 2.6 mm. Two specimens. Respiratory horn rather long, irregular. Prealar lobe short, two apical spines anteriorly directed. Mesonotal tubercle short, posterior to deep notch. Abdomen with dorsal tubercles inconspicuous.

Discussion

Since P. vespertilionis and P. isovespertilionis can be distinguished in the adult only from characters of the male genitalia, it would be necessary to rear some of the immature stages through to the adult if specific determination of the larval stage is to be made. Unfortunately,

in none of the cultures from which larvae were preserved did any survive to the adult stage. In cultures from which adults were obtained, the larvae of both species appeared identical. The two species are therefore treated together. The head is relatively large and the body slender. The larvae are very active, seldom remaining for long in one place. The antennae, while erect, are not on large tubercles, the dorsals are quite short, and the caudal setae are very long. In this combination of characters these species stand alone among all other species of which the larvae are known. Unfortunately, larvae of the other species of the vespertilionis group have not been obtained. Although the generally cylindrical body shape and whitish coloration would indicate that these species would be burrowers, the larvae generally remained on the surface of the food material in laboratory cultures. Larvae were found in natural habitats only on two occasions, each in soil and bat guano taken from inside hollow trees. These species were reared on several occasions with little difficulty on the regular food of feces, dead leaves and insect fragments.

Phlebotomus vexillarius Fairchild & Hertig

(Plate 23)

Fourth instar larva

Average length 4.3 mm. Three specimens.

Head. Frontal region prominent, evenly rounded as seen in lateral aspect. Antennal tubercle situated about mid-way between anterior and posterior frontal setae, somewhat prominent but not projecting beyond frontal profile, as seen in lateral aspect. Antenna erect, first segment short, wider than long; apical segment narrow and strongly bent

backward in middle. Integument covered with short, only slightly curved spicules; conspicuous pale areas around antennal tubercle and laterovertical seta where spicules are absent or sparse; spicules arranged in vague imbricated design posteriorly.

Thorax and abdomen. Nearly cylindrical. Integument covered with very small spicules which diminish in size posteriorly, not distinguishable on dorsum of abdomen.

Coloration. Head light brown, thorax and abdomen pale tan, with light brown patch on dorsum of eighth abdominal segment; caudal protuberance slightly darker.

Chaetotaxy. Head--Anterior and posterior frontals and dorsal and lateral verticals similar, weakly branched on distal half; dorsal vertical posterior to posterior frontal. Prothorax--Anterior setae similar, nearly equal in length, branched on distal half; posterior setae similar in structure, but internal dorsals directed posteriorly while external dorsals directed anteriorly, as in P. gomezi. Meso- and metathorax--Dorsals similar to those of posterior prothorax, laterodorsal longer, declinate. Abdomen--Setae like those of metathorax, but dorsals become progressively shorter posteriorly; those of segment VII very small and close to laterodorsal; posterior lateroventrals simple, long and slender on segment VII. Intersegmentaries small, not branched. External dorsal of segment VIII long, laterodorsal distinctly shorter; lateroventral small, reduced to simple microseta. Two pairs of caudal setae present, length 2.5 mm. Internal postanal not long, may be bent near apex; external postanal long, whip-like; lateroanal nearly as long as internal postanal, very slender at apex.

Pupa

Length 2.6 mm. One specimen. Respiratory horn long, irregular. Prealar lobe small and inconspicuous. Mesonotal tubercle very short, posterior to only slight depression. Abdomen without conspicuous dorsal tubercles.

Discussion

As already noted, this species shares certain characters with P. gomezi not found in any other species. The dorsal body setae are alternately directed anteriorly and posteriorly across the body, the antennae are erect but not on conspicuous tubercles, and the apical segment is strongly bent backward at its middle. It may be distinguished from P. gomezi by the shorter internal dorsals of abdominal segment VIII and the darker brown head capsule, as given in the key. Although its body is not at all flattened, it, like P. gomezi, is a surface-feeder. It was reared only once in the laboratory. Larvae were not found in natural habitats, and even adults were rarely encountered.

Phlebotomus ylephiletor Fairchild & Hertig

(Plate 24)

This species is very close to P. trapidoi, and a few small differences were noted only in the fourth instar, as follows: Anterior frontals more conspicuously branched; spicules on vertex more erect, not strongly curved forward. Two specimens.

Its habits are identical to those of P. trapidoi, as far as could be observed. Larvae were found in the same area as that species, on moist, dead leaves of the forest floor. This man-biting species has been reared with some difficulty many times in the laboratory.

Genus Warileya Hertig

Warileya rotundipennis Fairchild & Hertig

(Plate 25, Figs. i-k)

The immature stages of this genus have not previously been described. The three mounted specimens at hand do not show many details, but there are similarities to Phlebotomus. There are short setae on each body segment and two caudal setae. However, none of the setae appear to be brush-like. The head capsule is more globose than that of Phlebotomus, and the antenna is erect and posterior to the anterior frontal.

Although Hertig (1948) obtained engorged females of Warileya phlebotomanica in Peru, none of them oviposited. The same difficulty was encountered with W. rotundipennis in Panama. Adults of this species was found below the moist cloud forest of Cerro Campana, where they commonly fed on man during the late rainy season, September to December. Several engorged females were isolated in vials in the same manner as with Phlebotomus, but oviposition occurred with regularity only when the isolated females were left in the area where they were collected. Night temperatures there usually approximate 20° C. at that time of the year. Only a few of the eggs hatched, and the larvae refused to feed upon anything offered, including moist soil, algae, and the regular food of other species, consisting of feces, dead leaves and fragmented insects. The larvae died before sclerotization of the head capsule was completed.

Genus Nemopalpus

Nemopalpus sp.

(Plate 26)

Fourth instar larva

Length 8.5 mm. One specimen.

Head. Well developed, strongly sclerotized, antenna consisting of single structure nearly surrounded by membranous area, not projecting from head capsule, bearing several small pits or sensillae on outer surface; antenna located near oral margin, anterior to anterior frontal seta. Clypeus narrower than and continuous with frons, well sclerotized, prominent. Labrum a membranous lobe extending below clypeus, with a transverse sclerotized bar near its base; a seta at dorsal end of bar. Mandible heavily sclerotized with row of rounded teeth and prostheca-like structure ventrally and one long and one short seta dorsally. Maxilla transparent, lightly sclerotized, with several teeth and small setae apically; palpus short, with a few peg-like structures at apex. Ventrally a heavily sclerotized hypostome with five pairs of rounded teeth along distal margin. Labium represented by membranous, haired lobe dorsal to hypostome. Eyespot present, comprising a slightly raised area behind antenna. Setae as in Bruchomyia, differing from Phlebotomus in being entirely simple, posterior frontals outside of frontal area (posterior to frontal suture), and additional posterior seta (postoccipital) present.

Thorax and abdomen. Body cylindrical. Integument covered with conspicuous rounded tubercles, which are larger on summits of dorsal

prominences. Setae complex, consisting of central column topped by clear bulb-like structure, surrounded by several haired rods; setae more elongate posteriorly. Caudal setae no longer than abdominal segment VIII (including anal region), of a group of four setae on each side, one seta of each group slightly shorter than the rest; in life the four setae closely approximate so as to appear as a single seta. Arrangement of setae as in Bruchomyia and similar to that in Phlebotomus; anterior row of dorsal setae of five pairs, including anterior latero-dorsal. Abdomen without pseudopods, except on anal region, where the pseudopod is double and can be retracted. Ventral and posterior margin of anal protuberance with row of small crochets.

Coloration. Head dark brown; thorax and abdomen dark gray; eighth abdominal segment with dark brown dorsal patch, bifurcate posteriorly.

First instar larva

Average length 1.2 mm. Six specimens.

Much like fourth instar but head more acute anteriorly, as seen in dorsal aspect, dorsal and lateral setae of prothorax relatively longer, and caudal setae consisting of only one pair.

Discussion

This genus agrees closely with Satchell's (1953) description of Bruchomyia. The dorsal setae of the abdomen in Nemopalpus, however, appear to be shorter, and there is a row of crochet-like spines on the ventral margin of the anal protuberance, which Satchell does not show in Bruchomyia. Nemopalpus differs from Phlebotomus chiefly in the inconspicuous antennae, which do not protrude from the head, the presence of a small, pigmented eye spot, the absence of abdominal pseudopods

(except at the anal end), the compound structure of the body setae, and the structure of the caudal setae, each of which is actually a bundle of four setae which separate only when the larva is preserved.

Larvae were recovered from a soil sample taken at the base of a tree in the heavily forested Cerro Azul area. The sample was rich in organic debris, especially rotted wood and bark. Most of the larvae thrived on the regular food material used for Phlebotomus. All stages were very active and quickly crawled under the food material when disturbed. This is an apparently unnamed species.

LITERATURE CITED

Abonnenc, E. 1956. L'Oeuf et les formes pré-imaginales de deux Phlébotomes africains: P. antennatus var. occidentalis Theodor, 1933 et P. dubius Parrot, Mornet et Cadenat, 1945. Arch. Inst. Pasteur d'Algérie 34(4):518-539.

1956b. L'Oeuf et les formes larvavies de trois Phlebotomes africains: P. freetownensis sudanicus Theodor, 1933, P. freetownensis magnus Sinton, 1932 et P. schwetzi Adler, Theodor et Parrot, 1929. Arch. Inst. Pasteur d'Algérie 34(4):540-549.

Abonnenc, E. and M. Lariviére. 1957. Les formes larvaires de quelques Phlébotomes des régions méditerranéene et ethiopienne. Arch. Inst. Pasteur d'Algérie 35(4):391-403.

Addis, C. J. 1945. Laboratory rearing and life cycle of Phlebotomus (Dampfomvia) anthophorus Addis (Diptera, Psychodidae). Jour. Parasit. 31(5):319-322.

Barretto, M. P. 1940. Morphologia dos ovos das larvas e das pupas de Phlebotomus intermedius Lutz e Neiva, 1912 (Diptera, Psychodidae). An. Fac. Med. Univ. São Paulo 16:91-105.

1941. Morphologia dos ovos e das pupas de alguns flebótomos de São Paulo. An. Fac. Med. Univ. São Paulo 17:357-427.

1942. Contribuição para o estudo da biologia dos flebótomos em condições e perimentais. Tese de Doutoramento, Facultade de Medicina da Universidade de São Paulo, Cadeira de Parasitologia. 162 pp.

Castro, G.M.O. 1939. Hábitos de alguns flebótomos brasileiros. Jornal de Comercio (Rio de Janeiro) 112(81):4.

Chaniotis, B. N. and J. R. Anderson. 1964. Notes on the morphology and laboratory rearing of Phlebotomus vexator occidentis (Diptera, Psychodidae). Pan-Pacific Entomologist 40(1):27-32.

Colas-Belcour, J. 1928. Contribution à l'etude du développement et de la biologie des formes larvaires des phlébotomus. Thesis (Univ. of Paris) 93 pp.

Coutinho, J. O. and M. P. Barretto. 1941. Dados bionomicos sôbre o Phlebotomus fischeri Pinto 1926. Rev. Brasil. Biol. 1(4):423-429.

Deane, L. M. and M. P. Deane. 1957. Observações sobre abrigos e criadouros de flebótomos no noroeste do Estado do Ceará. Rev. Brasil. Malariol. Doencas Trop. 9(2):225-246.

Fairchild, G. B. 1949. A new fly related to Phlebotomus from Panama. Proc. Ent. Soc. Washington 51(2):81-84.

1955. The relationships and classification of the Phlebotominae (Diptera, Psychodidae). Ann. Ent. Soc. Amer. 48(3):182-196.

Fairchild, G. B. and M. Hertig. 1961. Notes on the Phlebotomus of Panama XVI (Diptera, Psychodidae), Descriptions of New and little-known species from Panama and Central America. Ann. Ent. Soc. Amer. 54(2):237-255.

Ferreira, L. C., L. Deane, and F. O. Mangabeira. 1938. Sôbre a biologia dos flebótomos dos zonas de leishmaniose visceral ora em estudo no Estado de Pará. O Hospital (Rio de Janeiro) 14:3-6.

Forattini, O. P. 1954. Algumas observaçõ̃es sôbre a biologia de flebótomos (Diptera, Psychodidae) em regiao de bacia do rio Paraná (Brasil). Arq. Fac. Hig. Saúde Publ. Univ. São Paulo 8:15-136.

Grassi, B. 1907. Ricerche sui flebotomi. Mem. Matematica Fisica, Soc. Ital. Sci. 14(3):353-394.

Hertig, M. 1942. Phlebotomus and carrious disease. Suppl. Amer. Jour. Trop. Med. 22:1-81.

1948. A new genus of bloodsucking psychodids from Peru. Ann. Ent. Soc. Amer. 41(1):8-16.

Hertig, M. and P. T. Johnson. 1961. The rearing of Phlebotomus sandflies (Diptera: Psychodidae) I. Technique. Ann. Ent. Soc. Amer. 54(6):753-764.

Howlett, F. M. 1913. The breeding places of Phlebotomus. Jour. Trop. Med. Hyg. 16:255-256.

Jerace, F. 1939. I Flebotomi degli Abruzzi. IIIa nota. (Distribuzione e biologia dei flebotomi in prov. di Teramo). Ann. Igiene 49(5):309-315.

Johnson, P. T. and M. Hertig. 1961. The rearing of Phlebotomus sandflies (Diptera: Psychodidae) II. Development and behavior of Panamanian sandflies in laboratory culture. Ann. Ent. Soc. Amer. 54(6):764-776.

Keilin, D. and P. Tate. 1937. A comparative account of the larvae of Trichomyia urbica Curtis, Psychodes albipennis Zett., and Phlebotomus argentipes Ann. & Brun. (Diptera: Psychodidae). Parasitology 29:247-258.

King, H. H. 1913. Notes on the bionomics of the sandflies (Phlebotomus) of Tokar, Anglo-Egyptian Sudan. Bull. Ent. Res. 4:83-84.

1914. Observations on the breeding places of sandflies (Phlebotomus spp.) in the Anglo-Egyptian Sudan. Jour. Trop. Med. Hyg. 17:2-3.

Lisova, A. I. 1931. The cycle of development of Phlebotomus chinensis Newstead. (In Russian). Mag. Parasit. Mus. Zool. Acad. Sci. URSS, 2:91-112. (Abstract in Rev. Appl. Ent. (B) 21:4, 1933.)

Mangabeira Filho, O. 1942a. 8.ª Contribuição ao estudo dos Flebotomus (Diptera, Psychodidae). Flebotomus (Brumptomyia) avellari Costa Lima, 1932. Mem. Inst. Oswaldo Cruz 37(2):225-240.

1942b. 9.ª Contribuição ao estude dos Flebotomus (Diptera, Psychodidae). Flebotomus (Pressatia) triacanthus Mangabeira, 1942. Mem. Inst. Oswaldo Cruz 37(2):241-250.

1942c. 10.ª Contribuição ao estudo dos Flebotomus (Diptera, Psychodidae). Flebotomus longispinus Mangabeira, 1942. Mem. Inst. Oswaldo Cruz 37(3):251-257.

1942d. 11.ª Contribução ao estudo dos Flebotomus (Diptera, Psychodidae). Flebotomus oswaldoi Mangabeira, 1942. Mem. Inst. Oswaldo Cruz 37(3):287-295.

1942e. 13.ª Contribuição ao estudo dos Flebotomus (Diptera, Psychodidae). Flebotomus (Brumptomyia) travassosi Mangabeira, 1942. Mem. Inst. Oswaldo Cruz 37(3):375-381.

Mangabeira Filho, O. and I. A. Sherlock. 1962. Sôbre o Phlebotomus brasiliensis Costa Lima, 1932 (Diptera, Psychodidae). Mem. Inst. Oswaldo Cruz 60(3):311-319.

Marett, P. J. 1910. Preliminary report on the investigation into the breeding places of the sandfly in Malta. Jour. Roy. Army Med. Corps. 15:268-291.

1913. The Phlebotomus flies of the Maltese Islands. Jour. Roy. Army Med. Corps. 20:162-171.

1915. The bionomics of the Maltese Phlebotomi. British Med. Jour. 1915. pp. 172-173.

McCombie-Young, T. C., A. E. Richmond, and G. R. Brendish. 1926. Sand-flies and sandfly fever in the Peshawar District. Indian Jour. Med. Res. 13:961-1021.

Mirsa, A. 1952. El desarrollo de Phlebotomus panamensis Shannon, 1926 y Ph. gomezi Nitzulescu, 1931 (Diptera, Psychodidae) en condiciones de laboratorio. Rev. Sanidad y Asistencia Social 16 (5,6):561-572.

Mitter, J. L. 1919. Preliminary report on an investigation into the breeding places of Phlebotomus (papatasii and minutus) in Lahore. Indian Jour. Med. Res. 6:452-461.

Mukerjee, S. 1931. On the Morphology of the terminal segments of Psychodidae larvae and their taxonomic importance, Indian Jour. Med. Res. 19:433-446.

Nájera, L. 1946. Observaciones sobre la ecologia de los phlebotomos en su fase larvaria principalmente. Rev. Ibérica Parasitol. 6(1-2):139-158.

Newstead, R. 1911-12. The papataci flies (Phlebotomus) of the Maltese Islands. Bull. Ent. Res. 2:47-78.

Parrot, L. 1932. Nouvelles observations sur la biologie de Phlebotomus papatasi (Scop.) Arch. Inst. Pasteur d'Algerie 10(3):407-409.

Patton, S. W. and E. Hindle. 1928. The north Chinese species of the genus Phlebotomus (Diptera, Psychodidae). Proc. Royal Soc. (B) 102:533-551.

Perfiljew, P. P. 1928. Beitrage zur anatomie der Phlebotomus-larven. Centralbl. f. Bakt. 107(4,5):296-305.

Petrishcheva, P. A. 1932. Contribution to the biology of Phlebotomus of the Karakala region of the Turkmen SSR. (In Russian.) Murghab Parasitol. Exped. 1930. Acad. Sci. USSR and Health Commissar Turkmen, in Trud. Sov. Izuch. proizvod. Sil. Ser. Turkmen, part 2:143-173, 6 figs., 24 refs. Leningrad Acad. Sci. (Abstract in Rev. Appl. Ent. (B) 21:98-99, 1933.)

1935. Faune, biologie et ecologie des Phlebotomes de la Turkomanie. (In Russian, with French summary.) In: Parasites, transmitteurs, animaux venimeux. Rec. Trav. 25e Anniv. Sci. Pavlovsky 1909-34, pp. 202-259, 8 figs., 1 folding map, 4 diagrams, 2 graphs, 12 refs. (Abstract in Rev. Appl. Ent. (B) 24:179-180, 1936.)

Petrishcheva, P. A., et al. 1949. Nests of birds as breeding places of sandflies (Phlebotomus). (In Russian.) Zool. Zhur. 28 (3):284-286. (Abstract in Rev. Appl. Ent. (B) 41:19, 1953.)

Petrishcheva, P. A. and I. M. Grokhovskaya. 1949. The burrow of the lamelliform-toothed rat Nesokia indica bailwardi (Thomas) as a site of mass breeding of sandflies (Phlebotomus). (In Russian.) Koklady Akad. Nauk SSSR (N.S.) 65(4):597-599. (Abstract in Rev. Appl. Ent. (B) 39:204, 1951.)

Petrishcheva, P. A. and V. V. Gubar. 1949. The breeding of Phlebotomus in the colonies of the large gerbil (Rhobomys opinus Licht.) (In Russian, with English summary.) Trav. Acad. Milit. Med. Kiroff Armee Rouge 25:243-254. (Abstract in Rev. Appl. Ent. (B) 34:78, 1946.)

Petrishcheva, P. A. and N. G. Izyumskaya. 1941. On breeding places of Phlebotomus in Sebastopol. (In Russian, with English summary.) Trav. Acad. Milit. Med. Kiroff Armee Rough 25:243-254. (Abstract in Rev. Appl. Ent. (B) 34:78, 1946.)

Pifano, F. 1941. La leishmaniosis tegumentaria en el Estado Yaracuy, Venezuela. Gaceta Med. Caracas 48:292-299.

Saccá, G. 1950. Stadi préimaginal di Phlebotomus perfiliewi Parrot, P. papatasi Scop., P. perniciosus Newstead (Diptera, Psychodidae). Rendiconti dell Instituto Superiore di Sanita 13:689-688.

1952. Descrizione dell uovo e degli stadii larvali di Phlebotomus (Prophlebotomus) minutus Rondani (Diptera, Psychodidae). Rendiconti dell Instututo Superiore di Sanita 15:381-394.

Satchell, G. H. 1953. On the early stages of Bruchomyia argentina Alexander. Proc. Roy. Ent. Soc. London (A) 28:1-12.

Schevtschenko, F. J. 1931. Die artmerkmale der larven von Phlebotomus papatasii, Phl. chinensis, Phl. sergenti und Phl. caucasici (Marzinovsky) s. li (Popoff). Arch. Schiffs-u. Tropenhyg. 35(9):526-537.

Sherlock, I. A. 1957. Sôbre o Phlebotomus lenti Mangabeira 1938 (Diptera, Psychodidae). Rev. Brasil. Biol. 17(1):77-88.

1957b. Sôbre o Phlebotomus renei Martins, Falcão and Silva 1956 (Diptera, Psychodidae). Rev. Brasil. Biol. 17(4):547-556.

Sherlock, I. A., and M. Carneiro. 1963. Descrição das fases imaturas do Phlebotomus bahiensis Mangabeira & Sherlock 1961 (Diptera, Psychodidae). Mem. Inst. Oswaldo Cruz 61(3):491-494.

Shortt, H. E., R. O. A. Smith, and C. S. Swaminath. 1930. The breeding in nature of Phlebotomus argentipes, Ann. and Brun. Bull. Ent. Res. 21:269-271.

1932. Miscellaneous experiments with Phlebotomus argentipes in relation to transmission of kala-azar. Indian Med. Res. Mem. No. 25:90-102.

Smith, R. O. A., K. V. Krishman, and S. Mukerjee. 1934. Identification of larvae of the genus Phlebotomus. Indian Jour. Med. Res. 21(4): 661-667.

Smith, R. A. O., S. Mukerjee, and C. Lal. 1936. Bionomics of P. argentipes. Part II. The breeding sites of P. argentipes and an attempt to control these insects by anti-larval measures. Indian Jour. Med. Res. 24(2):557-562.

Theodor, Oskar. 1948. Classification of the Old World species of the subfamily Phlebotominae. Bull. Ent. Res. 39:85.

1965. On the classification of American Phlebotominae. Jour. Med. Ent. 2(2):171-197.

Wanson, M. 1942. Sur la biologie des phlébotomes congolais. Rec. Trav. Sci. Med. Congo Belge 1942 (1):23-43.

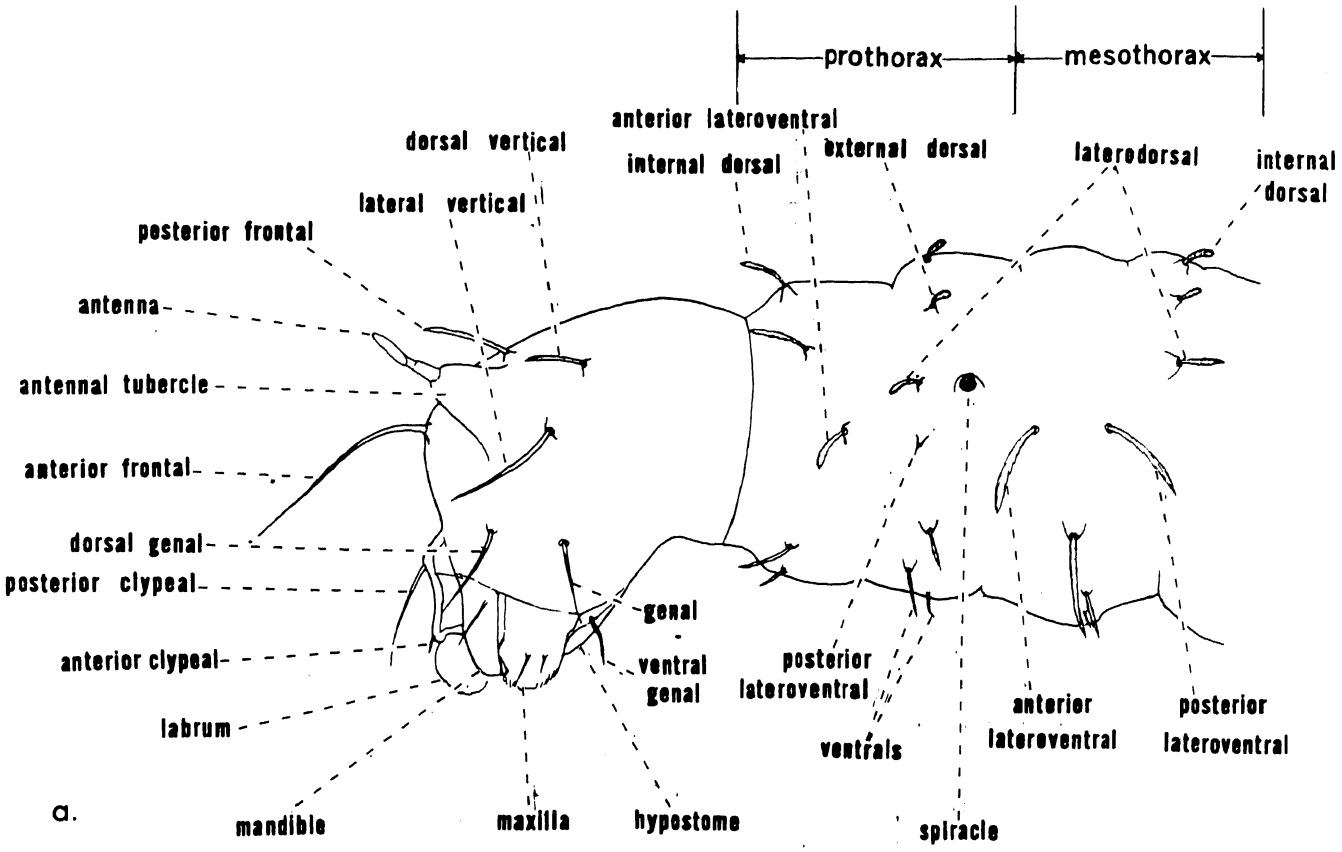
Whittingham, H. E. and A. F. Rook. 1923. Observations on the life history and bionomics of Phlebotomus papatasii. British Med. Jour. No. 3285:1144-51.

PLATE 1

Fourth instar larva of Phlebotomus, semidiagrammatic

Figure a. Head, prothorax and mesothorax.

Figure b. Posterior end of abdomen.


prothorax
mesothorax
anterior lateroventral
dorsal vertical
internal dorsal
external dorsal
laterodorsal
internal dorsal
lateral vertical
posterior frontal
antenna
antennal tubercle
anterior frontal
dorsal genal
posterior clypeal
anterior clypeal
labrum
genal
ventral genal
posterior lateroventral
ventrals
anterior lateroventral
posterior lateroventral
a.
mandible
maxilla
hypostome
spiracle

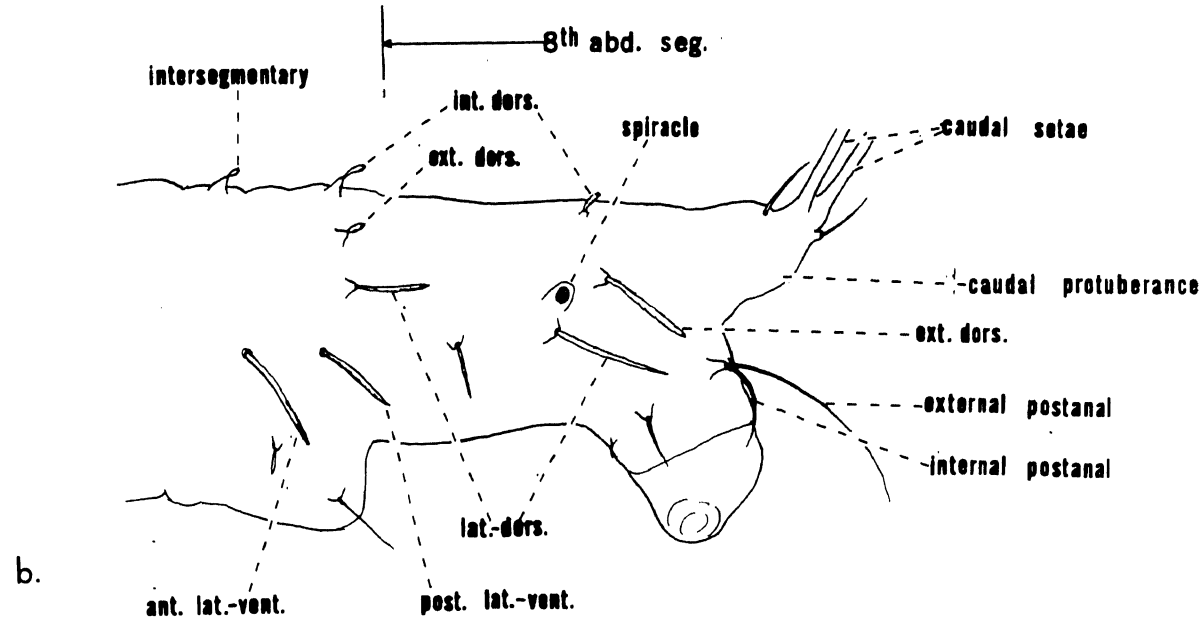
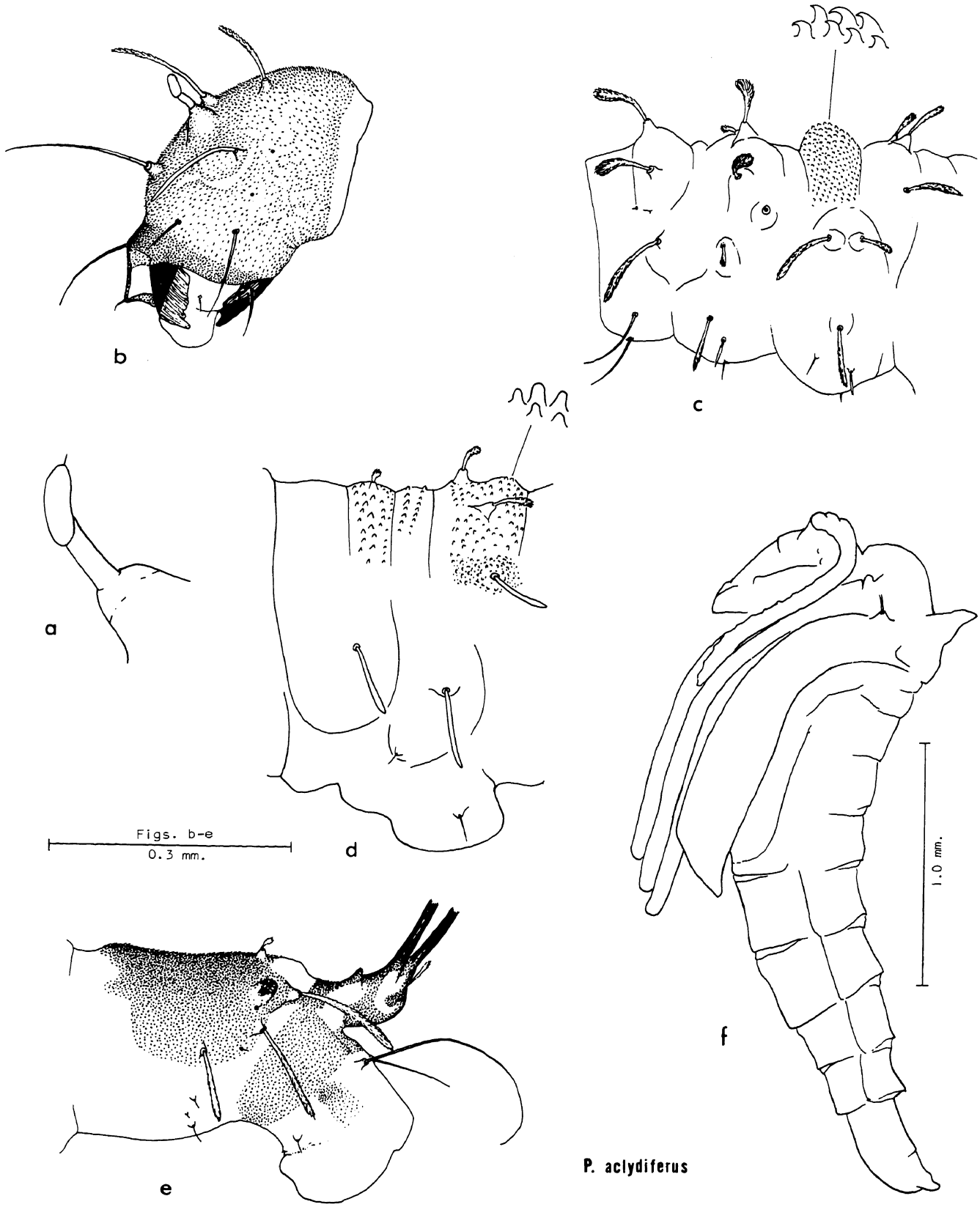

8th abd. seg.
intersegmentary
int. dors.
ext. dors.
spiracle
caudal setae
caudal protuberance
ext. dors.
external postanal
internal postanal
lat.-dors.
b.
ant. lat.-vent.
post. lat.-vent.

PLATE 2

Phlebotomus aclydiferus

Figures a - e. Fourth instar larva (a. Antenna, b. Head, c. Prothorax and mesothorax, d. Third abdominal segment, e. Eighth abdominal segment.)

Figure f. Pupa.



P. aclydiferus

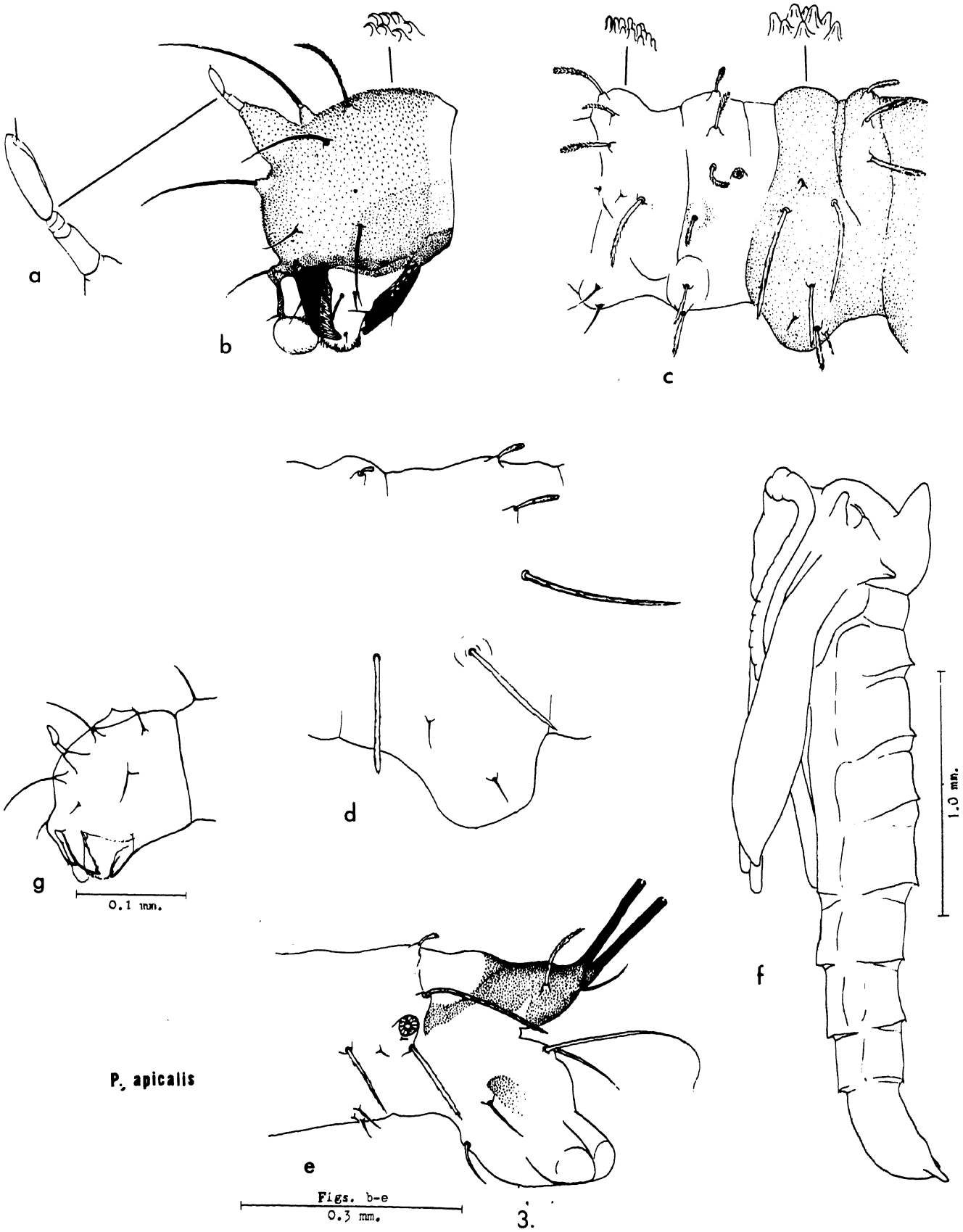
PLATE 3

Phlebotomus apicalis

Figures a - e. Fourth instar larva (a. Antenna, b. Head, c. Prothorax and mesothorax, d. Third abdominal segment, e. Eighth abdominal segment.)

Figure f. Pupa.

Figure g. Head of first instar larva.



3.

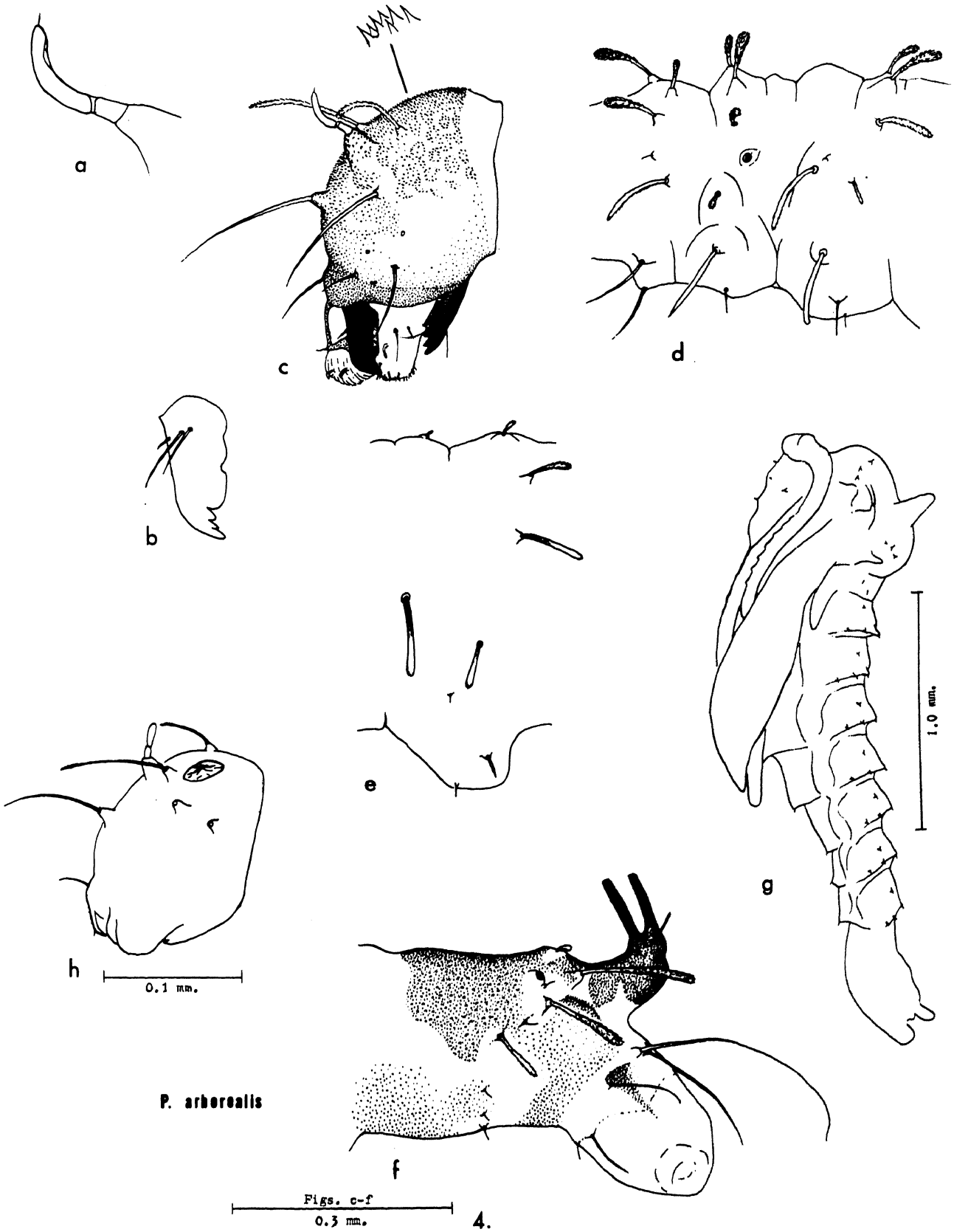
PLATE 4

Phlebotomus arborealis

Figures a - f. **Fourth instar larva (a. Antenna, b. Mandible, c. Head, d. Prothorax and Mesothorax, e. Third abdominal segment, f. Eighth abdominal segment.)**

Figure g. **Pupa.**

Figure h. **Head of first instar larva**, slightly rotated. Antenna and setae of left side not shown.



P. arboreallis

Figs. c-f
0.3 mm.

4.

PLATE 5

Phlebotomus camposi

Figures a - d. Fourth instar larva (a. Head, b. Prothorax and mesothorax, c. Third abdominal segment, d. Eighth abdominal segment.)

Figs. a-d
0.3 mm.

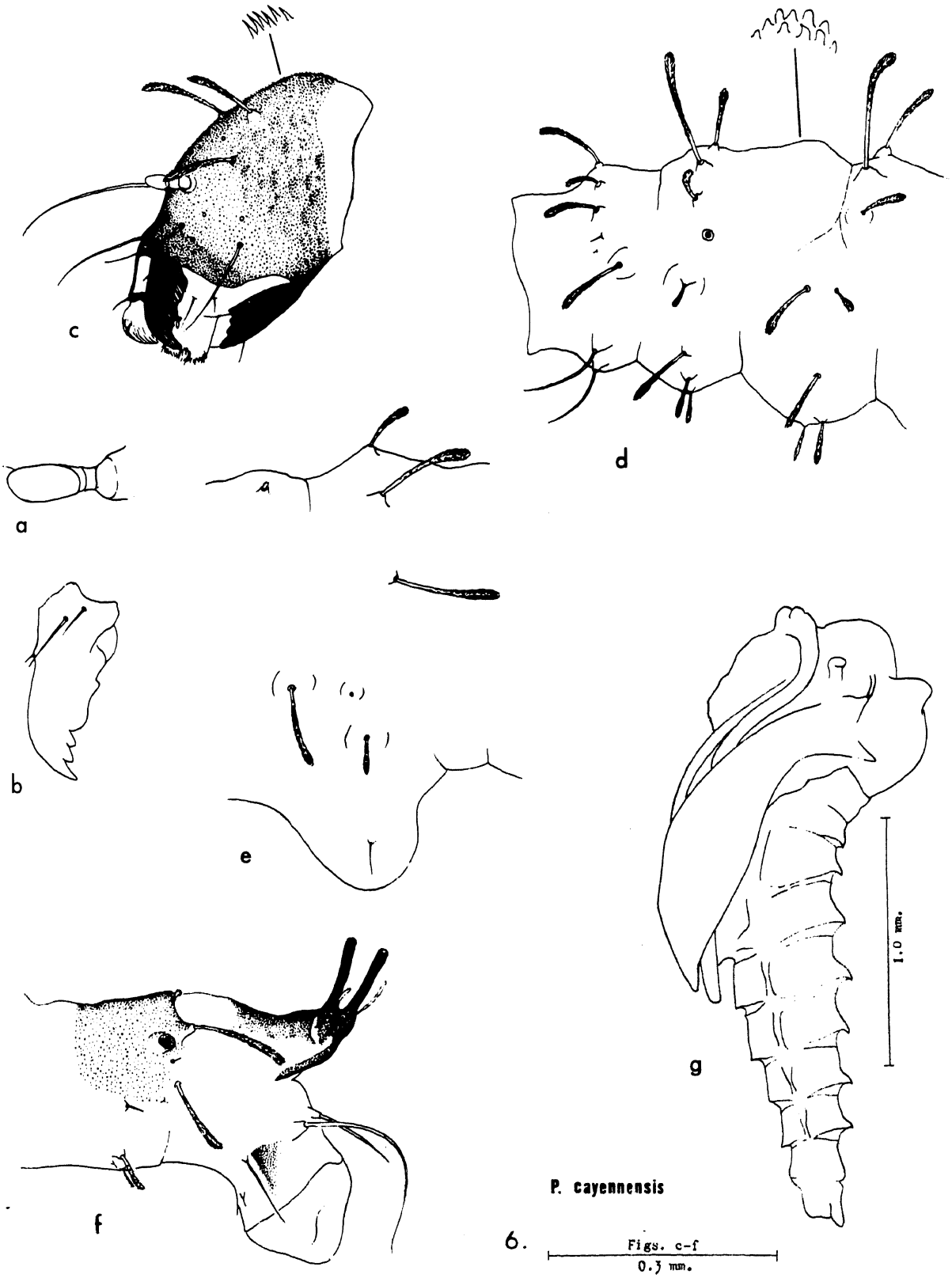
P. camposi

PLATE 6

Phlebotomus cayennensis

Figures a - f. Fourth instar larva (a. Antenna, b. Mandible, c. Head, d. Prothorax and mesothorax, e. Third abdominal segment, f. Eighth abdominal segment.)

Figure g. Pupa.



P. cayennensis

6. Figs. c-f
0.3 mm.

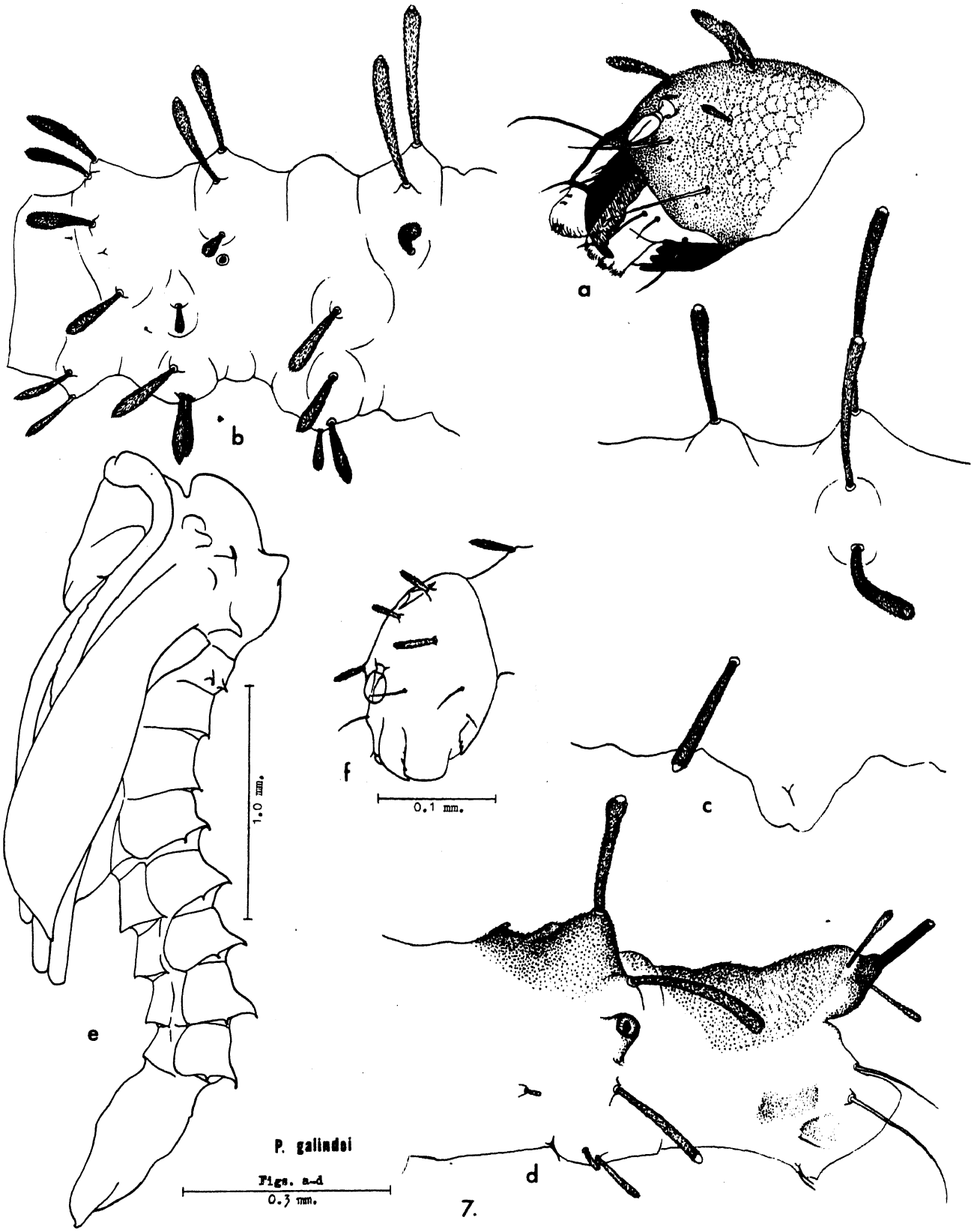
PLATE 7

Phlebotomus galindoi

Figures a - d. Fourth instar larva (a. Head, b. Prothorax and mesothorax, c. Third abdominal segment, d. Eighth abdominal segment.)

Figure e. Pupa.

Figure f. Head of first instar.

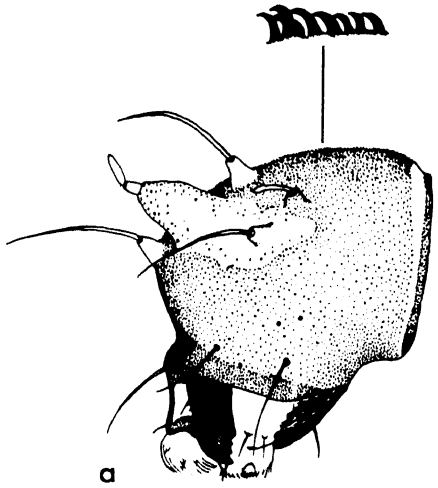


7.

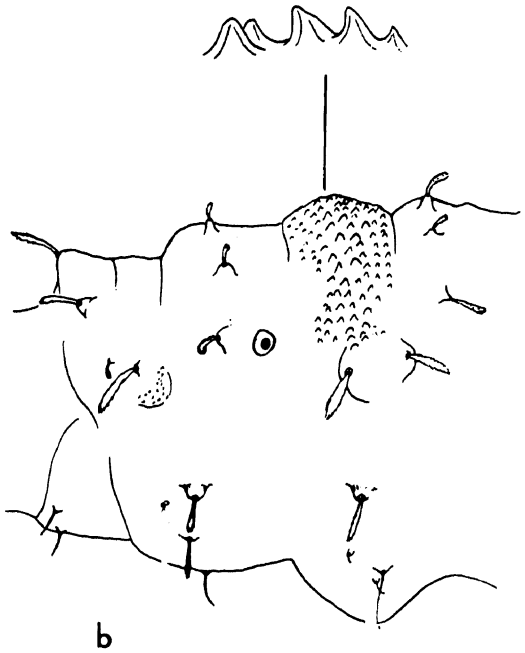
PLATE 8

Phlebotomus geniculatus

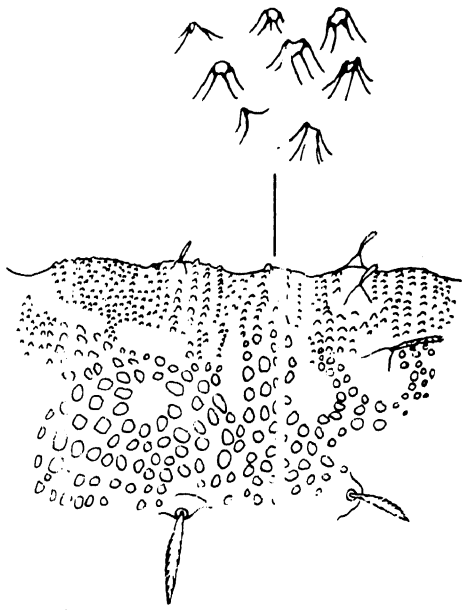
Figures a - d. Fourth instar larva (a. Head, b. Prothorax and mesothorax, c. Third abdominal segment, d. Eighth abdominal segment.)



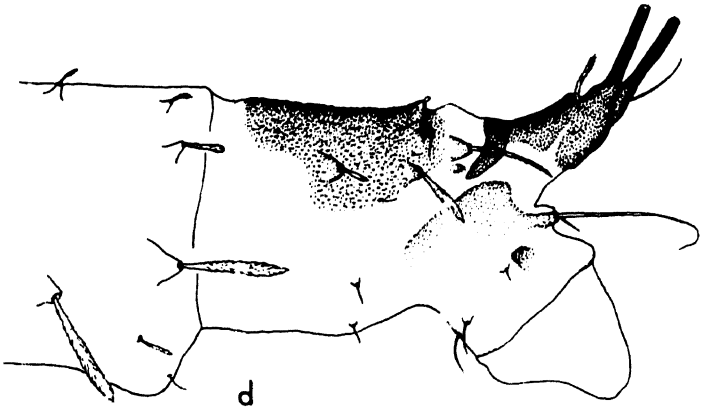
a



b



c



d

Figs. a-d
0.3 mm.

P. geniculatus

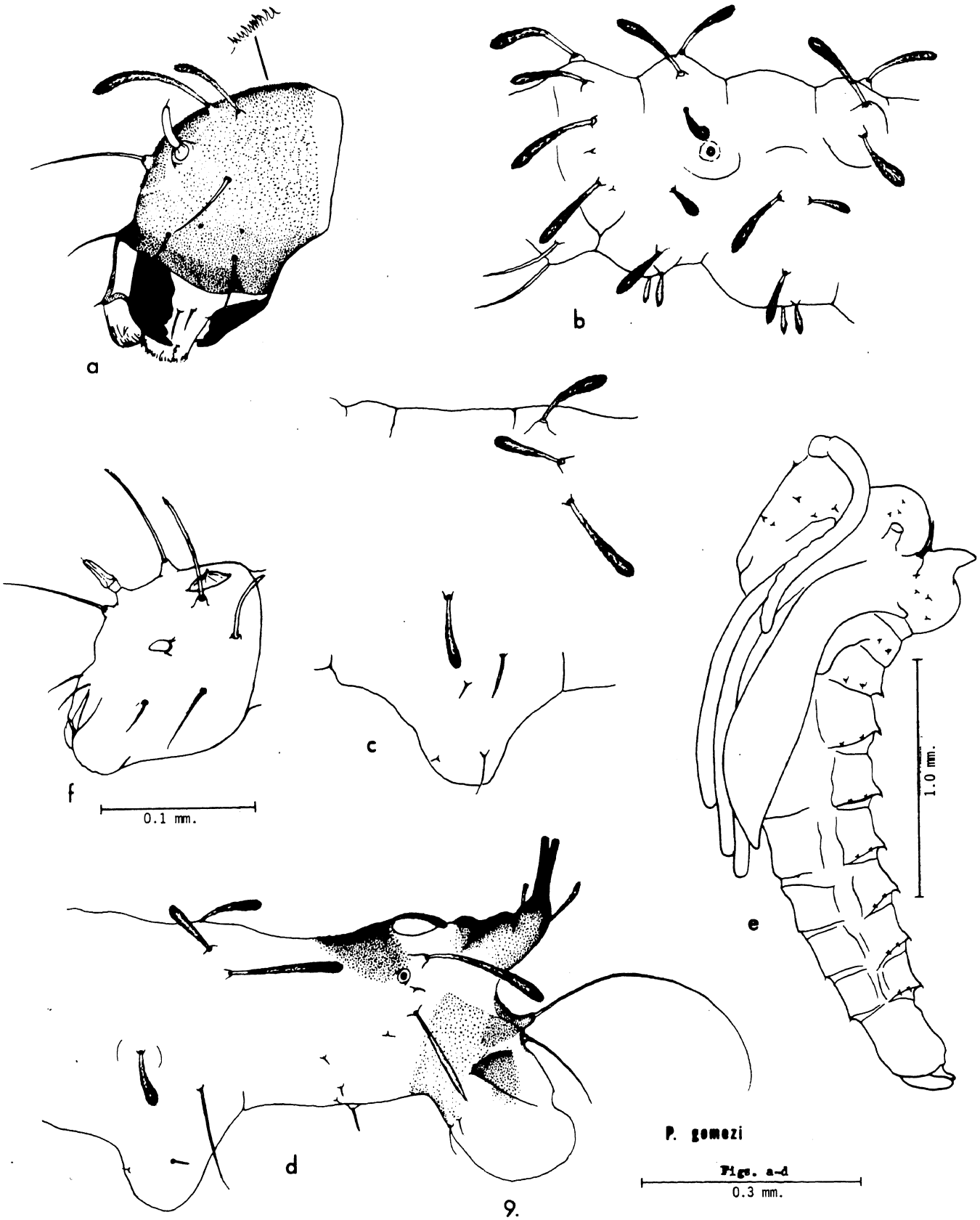
PLATE 9

Phlebotomus gomezi

Figures a - d. Fourth instar larva (a. Head, b. Prothorax and mesothorax, c. Third abdominal segment, d. Seventh and eighth abdominal segments.)

Figure e. Pupa.

Figure f. Head of first instar larva, slightly rotated.



P. gomezi

Figs. a-d

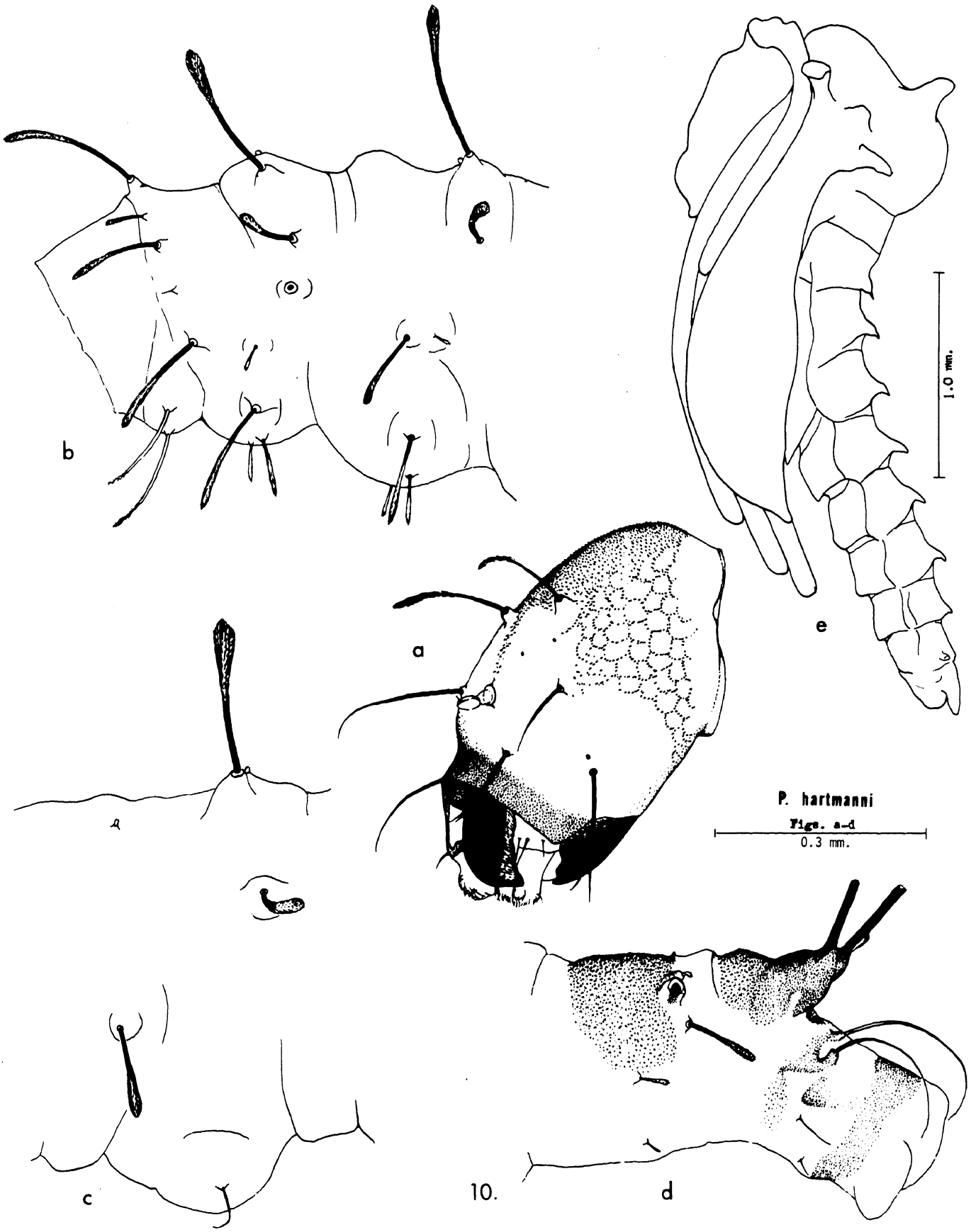
0.3 mm.

PLATE 10

Phlebotomus hartmanni

Figures a - d. Fourth instar larva (a. Head, b. Prothorax and mesothorax, c. Third abdominal segment, d. Eighth abdominal segment.)

Figure e. Pupa.



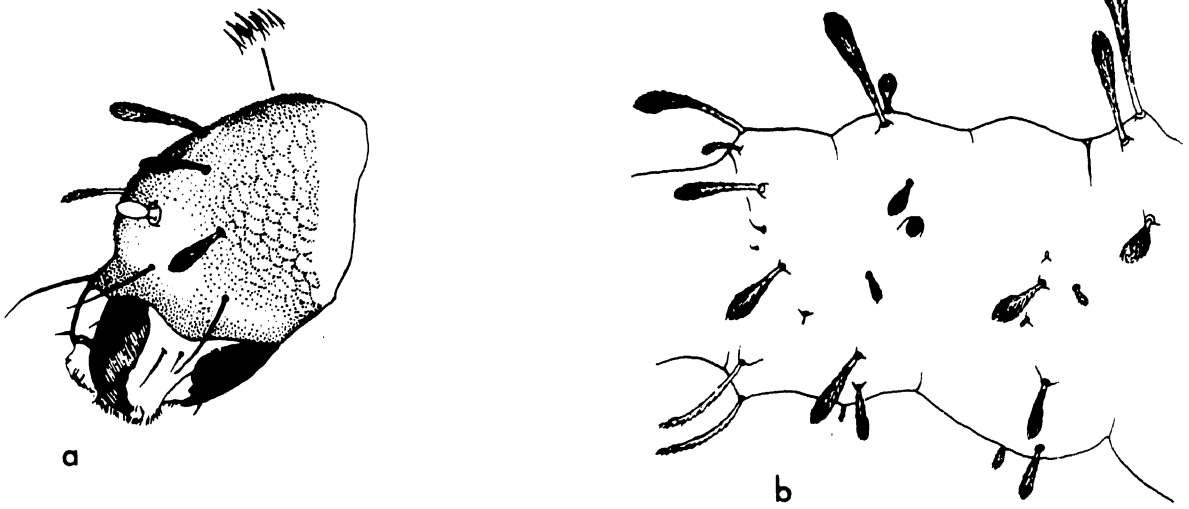
10.

PLATE 11

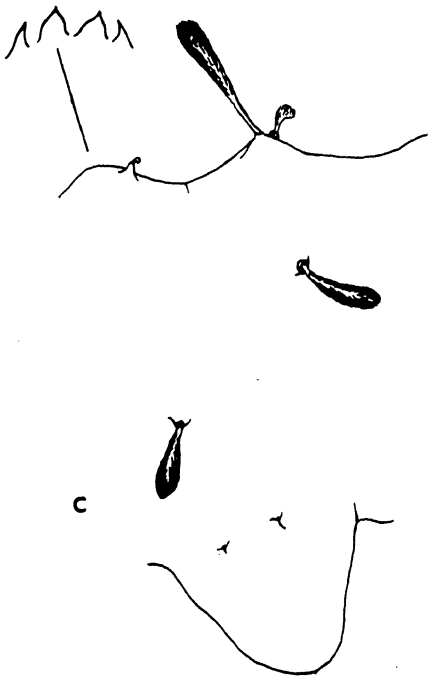
Phlebotomus ovallesi

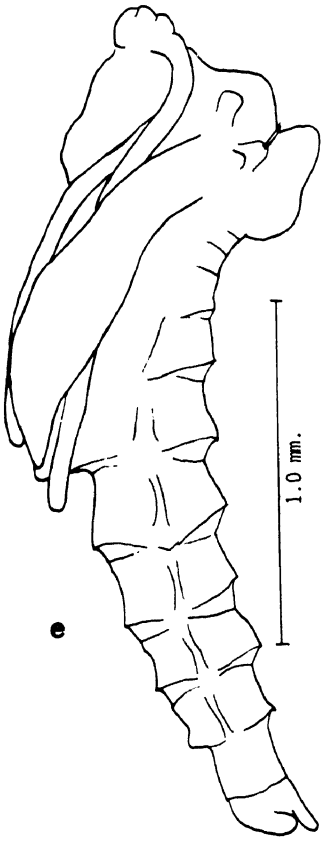
Figures a - d. Fourth instar larva (a. Head, b. Prothorax and mesothorax, c. Third abdominal segment, d. Eighth abdominal segment.)

Figure e. Pupa.



Figs. a-d
0.3 mm.





P. ovallesi

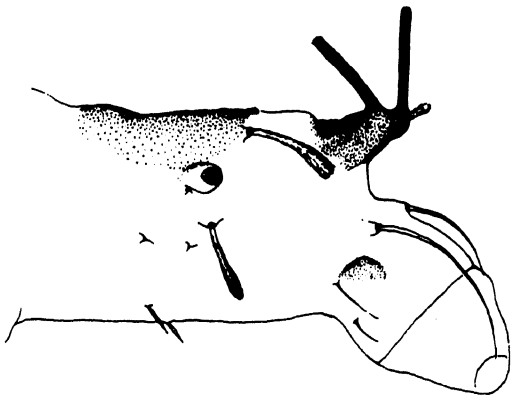


PLATE 12

Phlebotomus panamensis

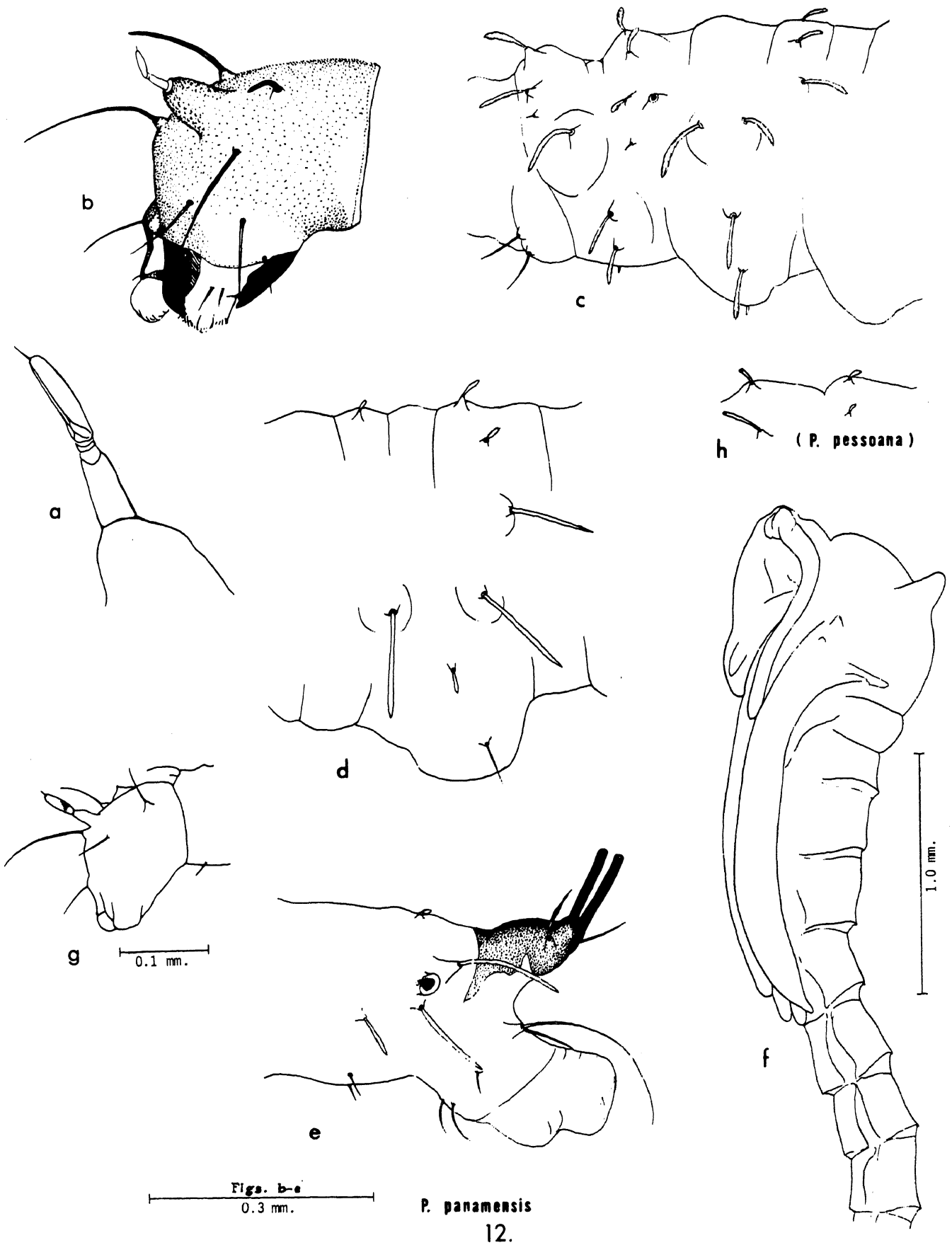
Figures a - e. Fourth instar larva (a. Antenna, b. Head, c. Prothorax and mesothorax, d. Third abdominal segment, e. Eighth abdominal segment.)

Figure f. Pupa.

Figure g. Head of first instar larva.

Phlebotomus pessoana

Figure h. Fourth instar larva, dorsal region of prothorax.



Figs. b-e
0.3 mm.

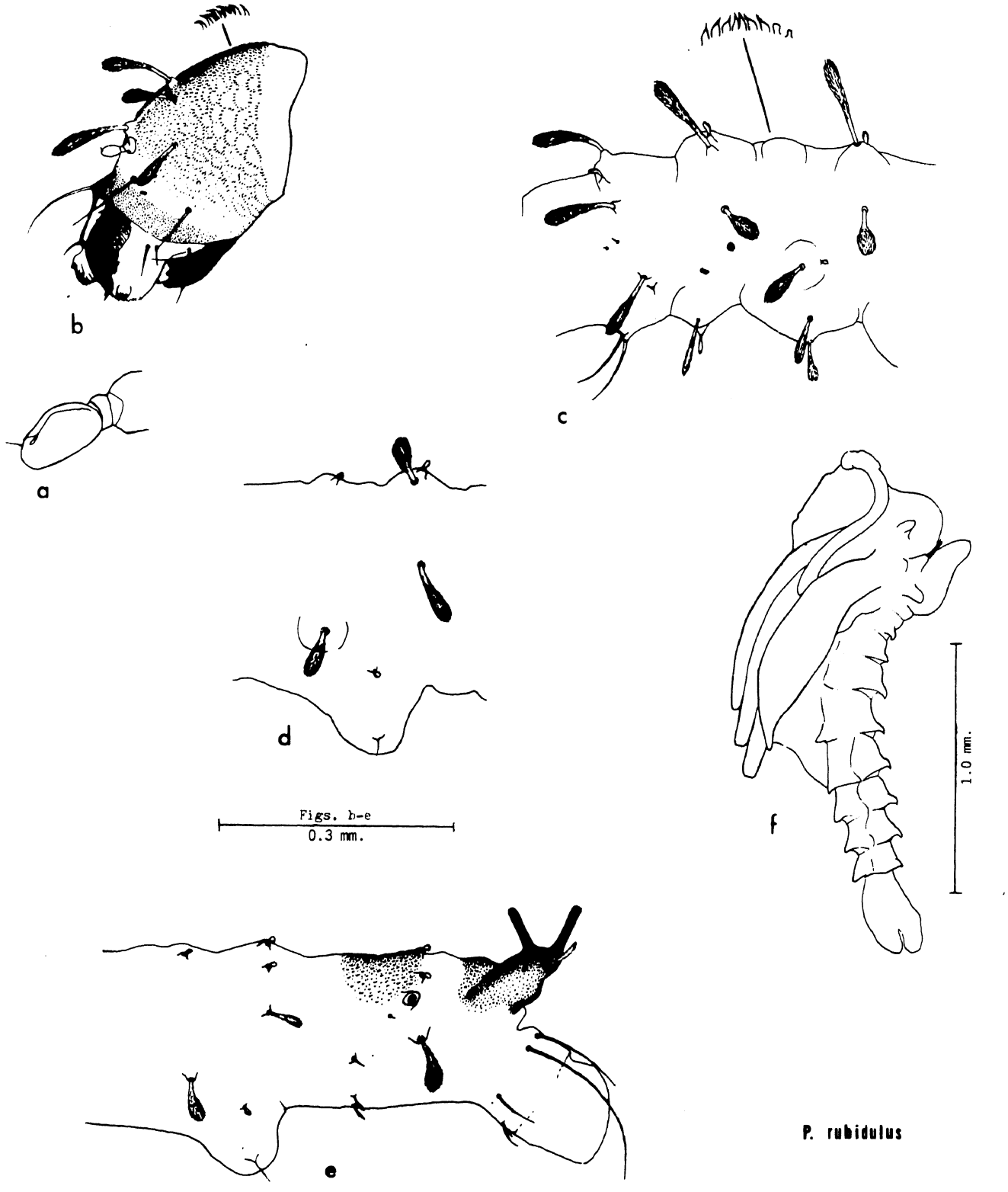
P. panamensis

PLATE 13

Phlebotomus rubidulus

Figures a - e. Fourth instar larva (a. Antenna, b. Head, c. Prothorax and mesothorax, d. Third abdominal segment, e. Seventh and Eighth abdominal segment.)

Figure f. Pupa.



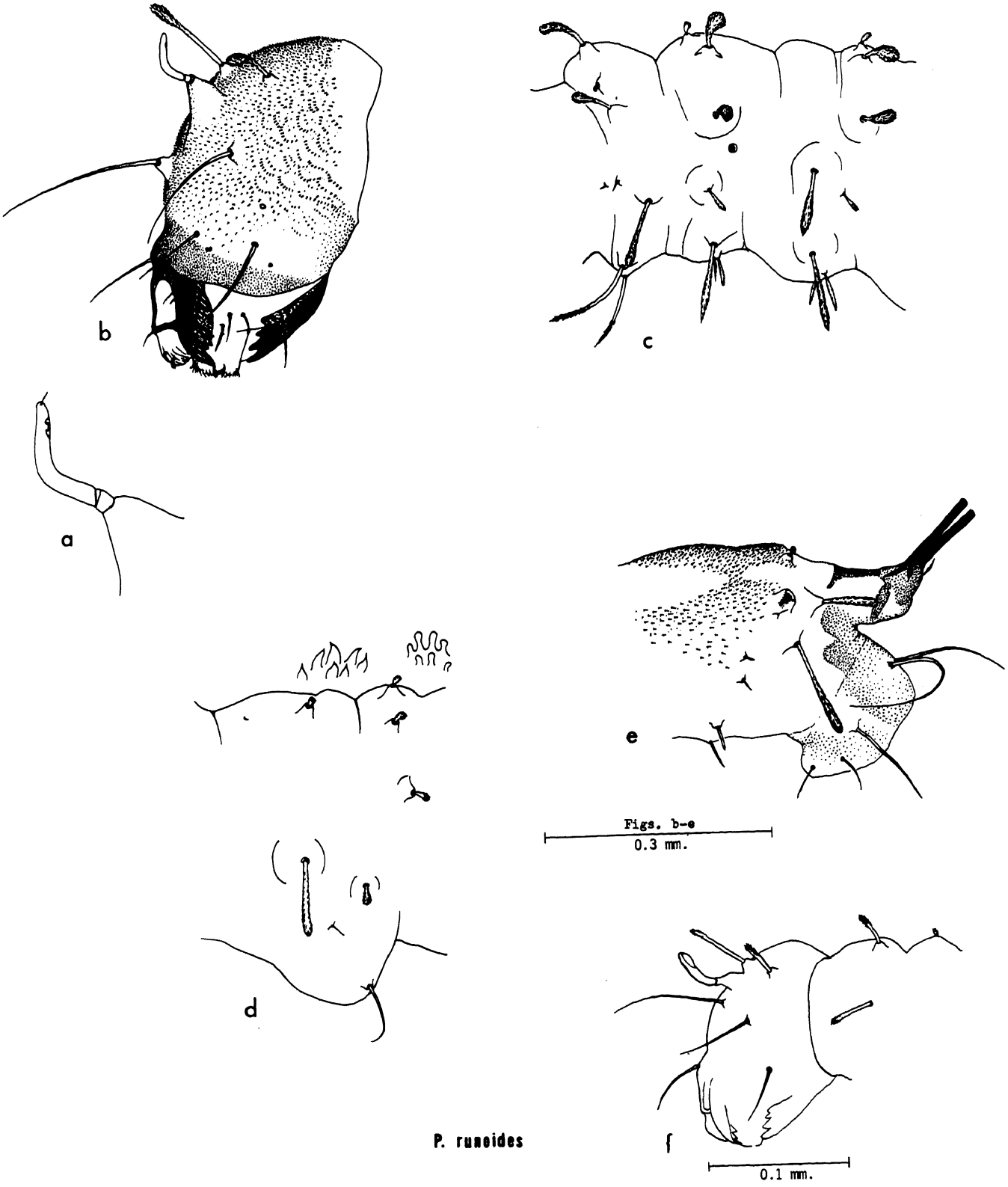
P. rubidulus

PLATE 14

Phlebotomus runoides

Figures a - e. Fourth instar larva (a. Antenna, b. Head, c. Prothorax and mesothorax, d. Third abdominal segment, e. Eighth abdominal segment.)

Figure f. Head and prothorax of first instar larva.



P. runcides

PLATE 15

Phlebotomus sanguinarius

Figures a - d. Fourth instar larva (a. Head, b. Prothorax and mesothorax, c. Third abdominal segment, d. Eighth abdominal segment.)

Figure e. Pupa.

Figure f. Head of first instar larva.

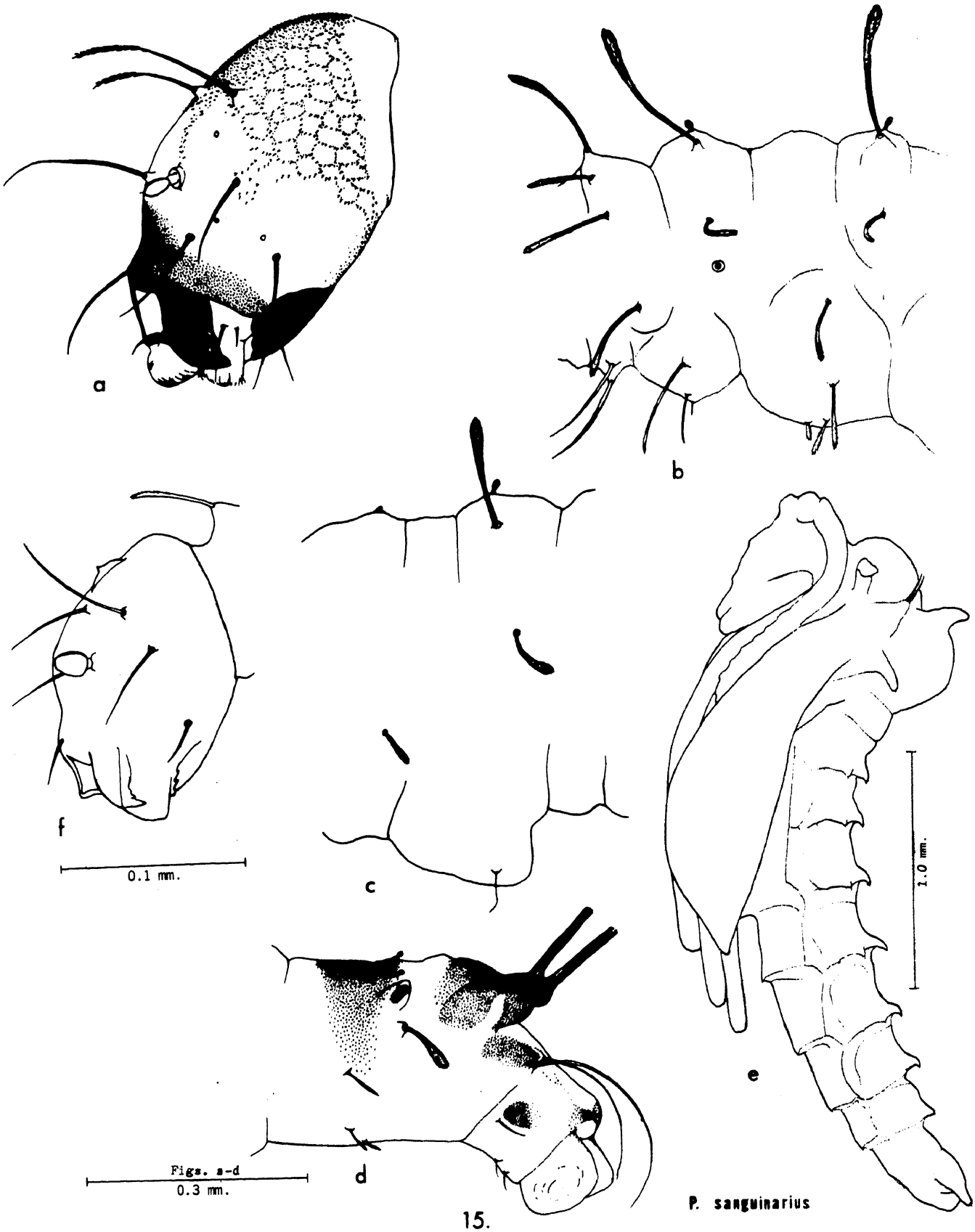

a
b
c
d
e
f
0.1 mm.
1.0 mm.
Figs. a-d
0.3 mm.
P. sanguinarius

PLATE 16

Phlebotomus serranus

Figures a - e. Fourth instar larva (a. Antenna, b. Head, c. Prothorax and mesothorax, d. Third abdominal segment, e. Eighth abdominal segment.)

Figure f. Pupa.

P. serranus

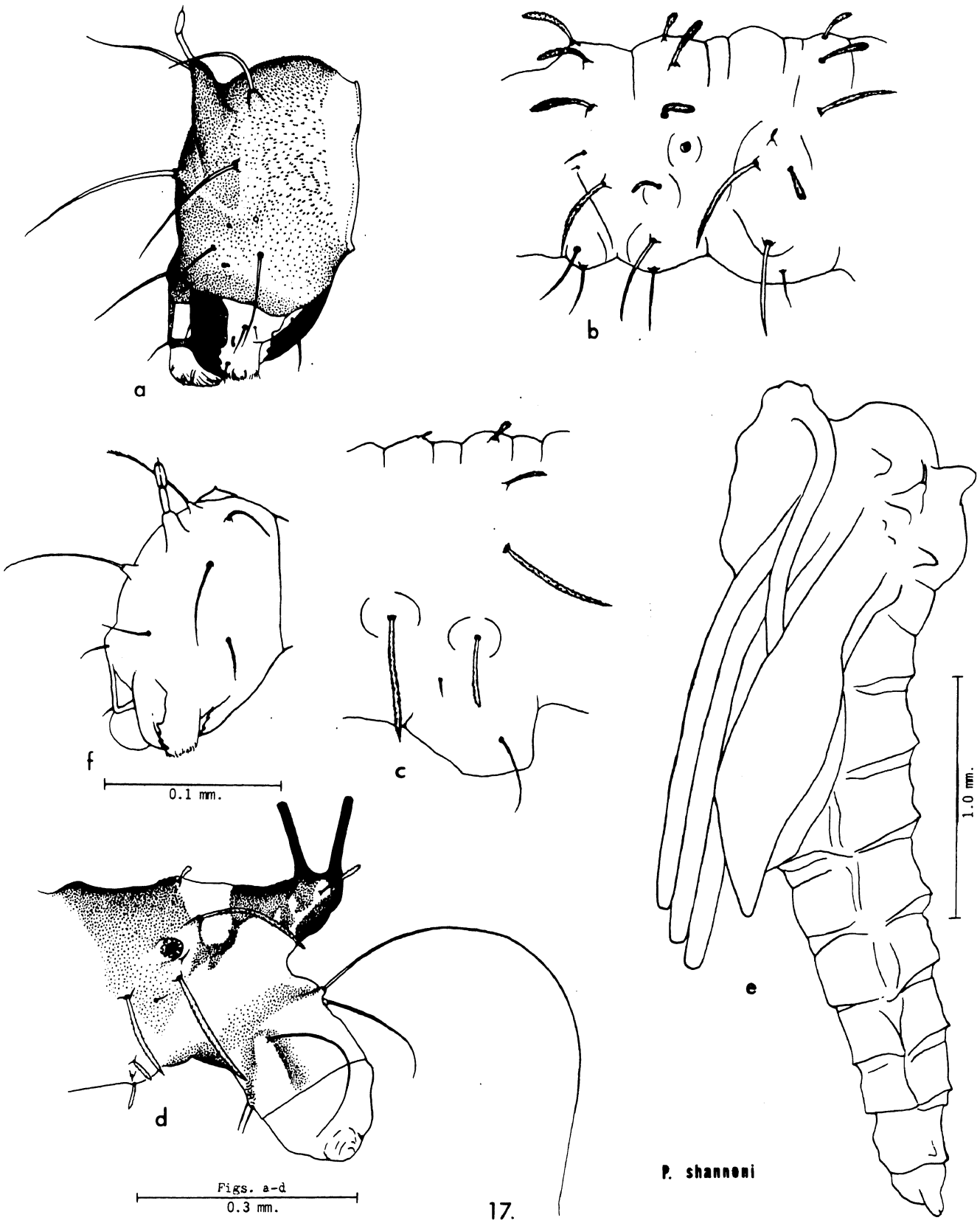
PLATE 17

Phlebotomus shannoni

Figures a - d. Fourth instar larva (a. Head, b. Prothorax mesothorax, c. Third abdominal segment, d. abdominal segment.)

Figure e. Pupa.

Figure f. Head of first instar larva.



Figs. a-d
0.3 mm.

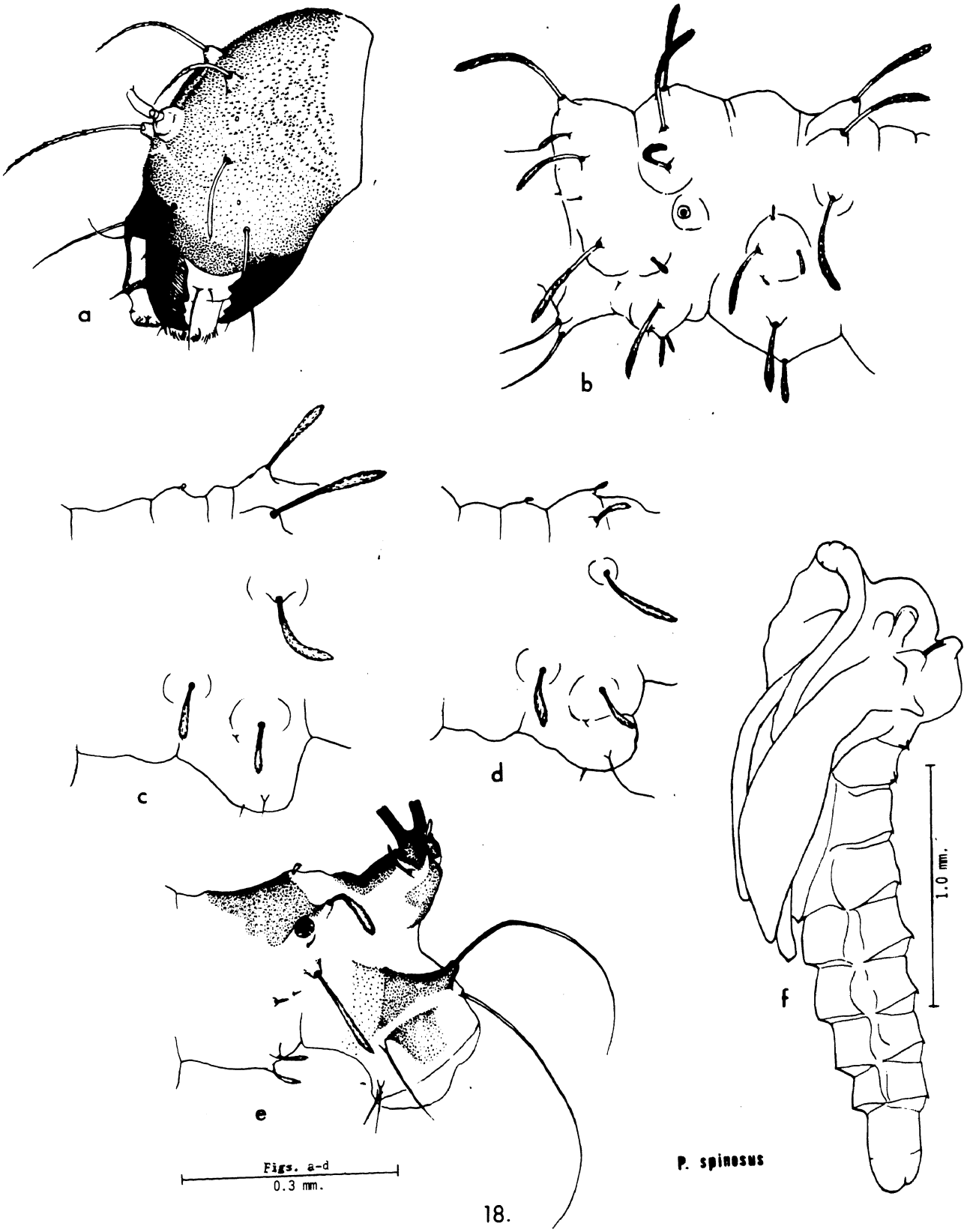
P. shannoni

PLATE 18

Phlebotomus spinosus

Figures a - e. Fourth instar larva (a. Head, b. Prothorax and mesothorax, c. Third abdominal segment, d. Seventh abdominal segment, e. Eighth abdominal segment.)

Figure f. Pupa.



P. spinosus

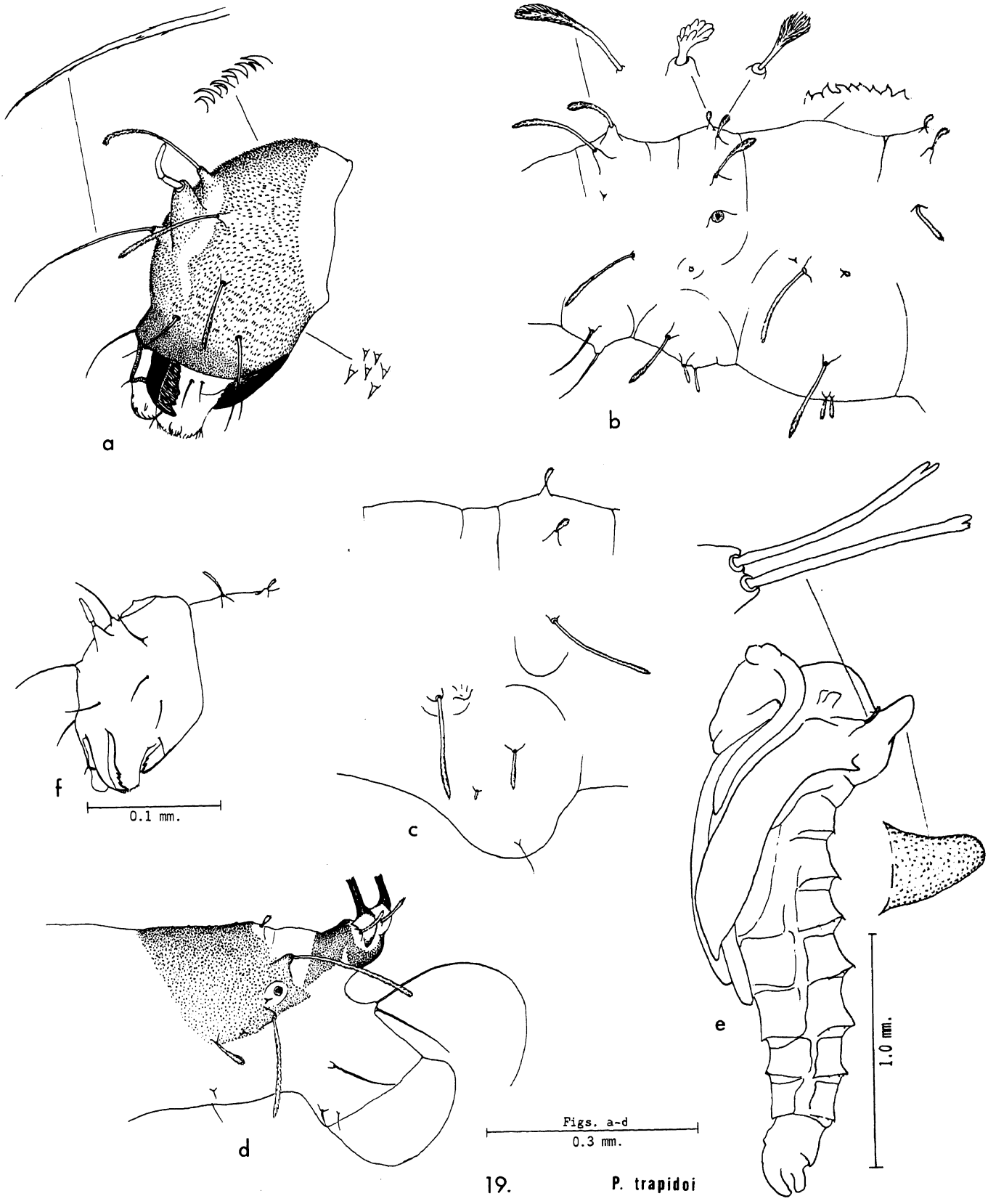
PLATE 19

Phlebotomus trapidoi

Figures a - d. Fourth instar larva (a. Head, b. Prothorax and mesothorax, c. Third abdominal segment, d. Eighth abdominal segment.)

Figure e. Pupa.

Figure f. Head of first instar larva.



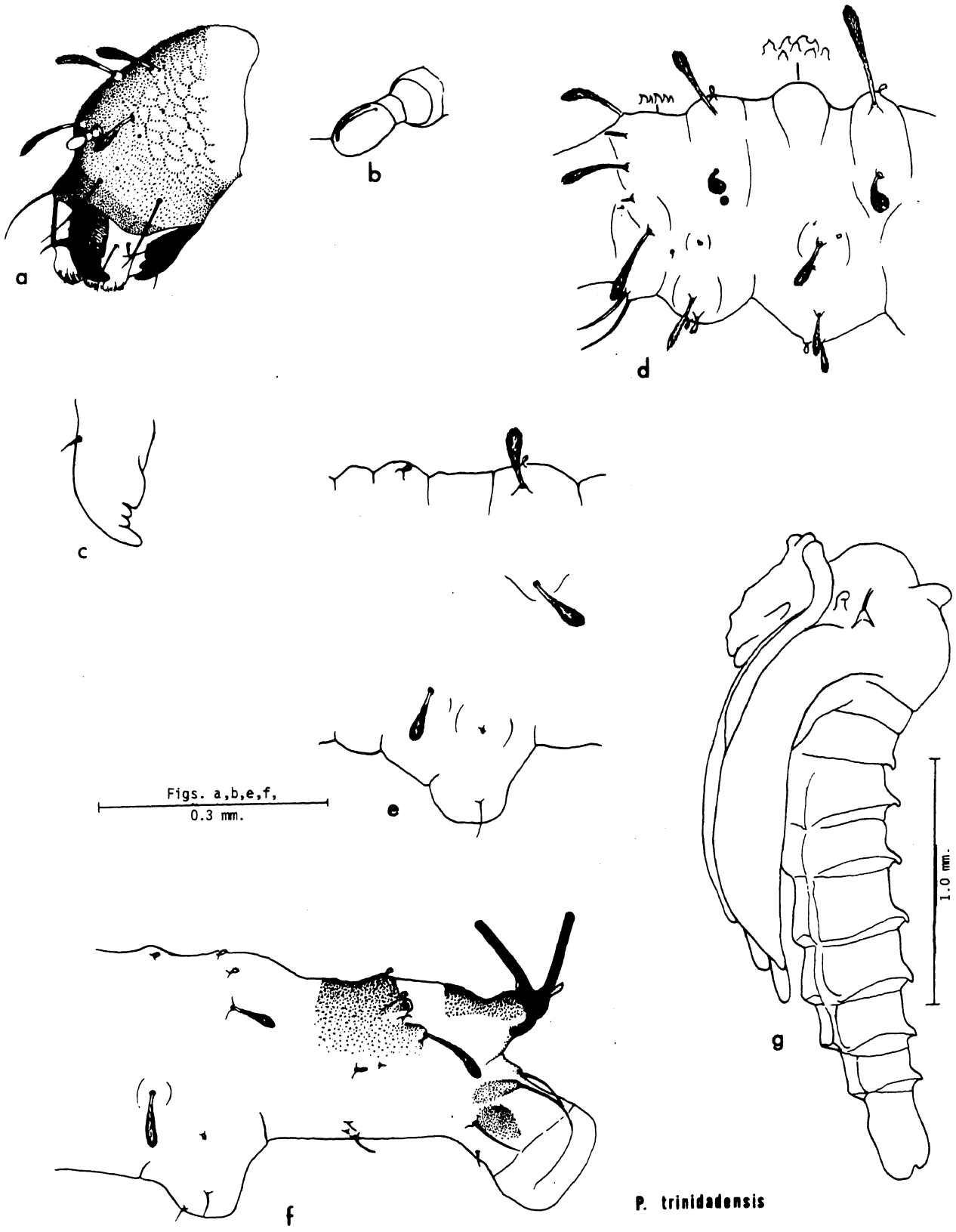
19. P. trapidoi

PLATE 20

Phlebotomus trinidadensis

Figures a - f. Fourth instar larva (a. Head, b. Antenna, c. Mandible, d. Prothorax and mesothorax, e. Third abdominal segment, f. Seventh and eighth abdominal segments.)

Figure g. Pupa.



P. trinidadensis

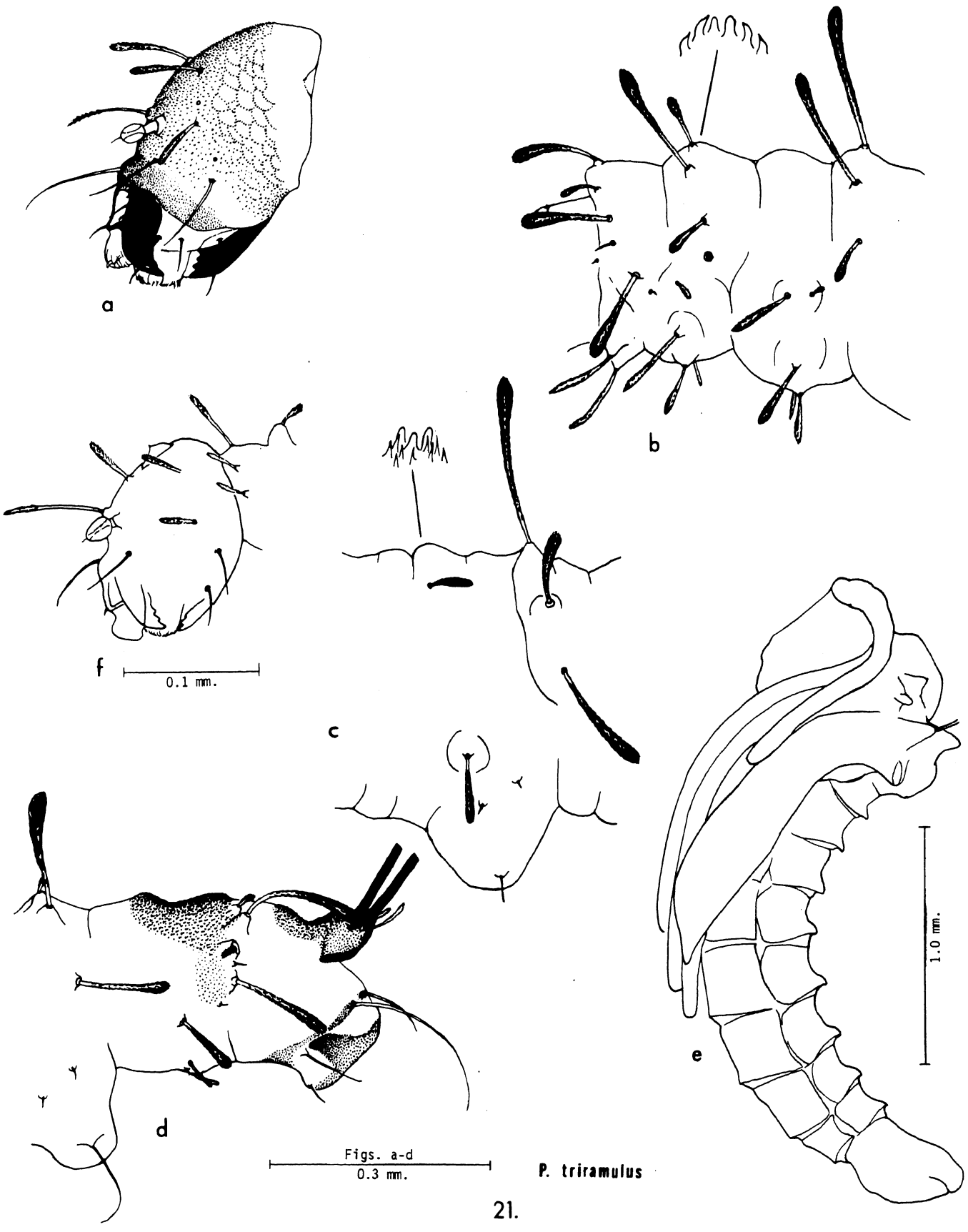
PLATE 21

Phlebotomus triramulus

Figures a - d. Fourth instar larva (a. Head, b. Prothorax and mesothorax, c. Third abdominal segment, d. Seventh and eighth abdominal segments.)

Figure e. Pupa.

Figure f. Head of first instar larva.



P. triramulus

PLATE 22

Phlebotomus vespertilionis

Figures a - e. Fourth instar larva (a. Antenna, b. Head, c. Prothorax and mesothorax, d. Third abdominal segment, e. Eighth abdominal segment.)

Figure f. Pupa.

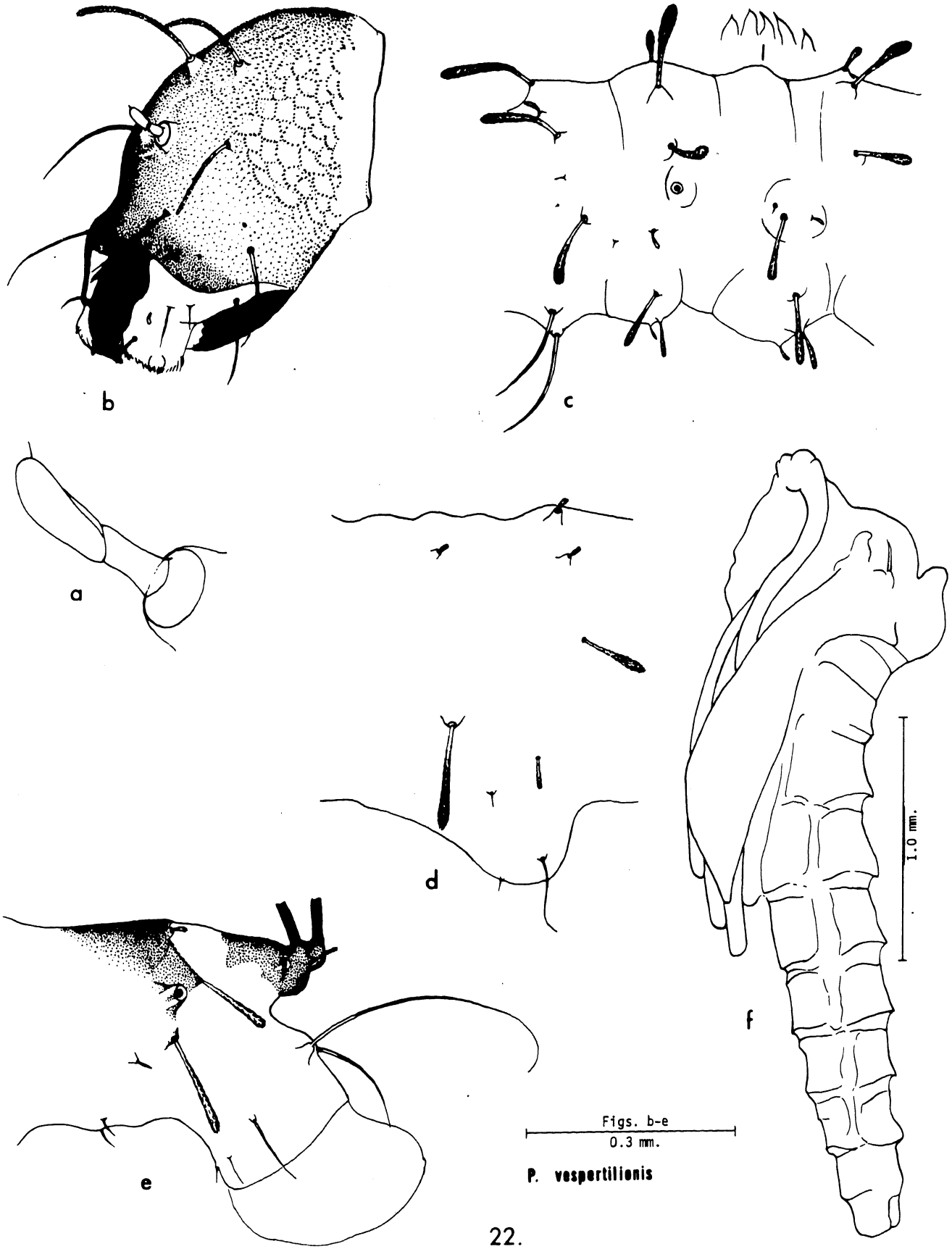
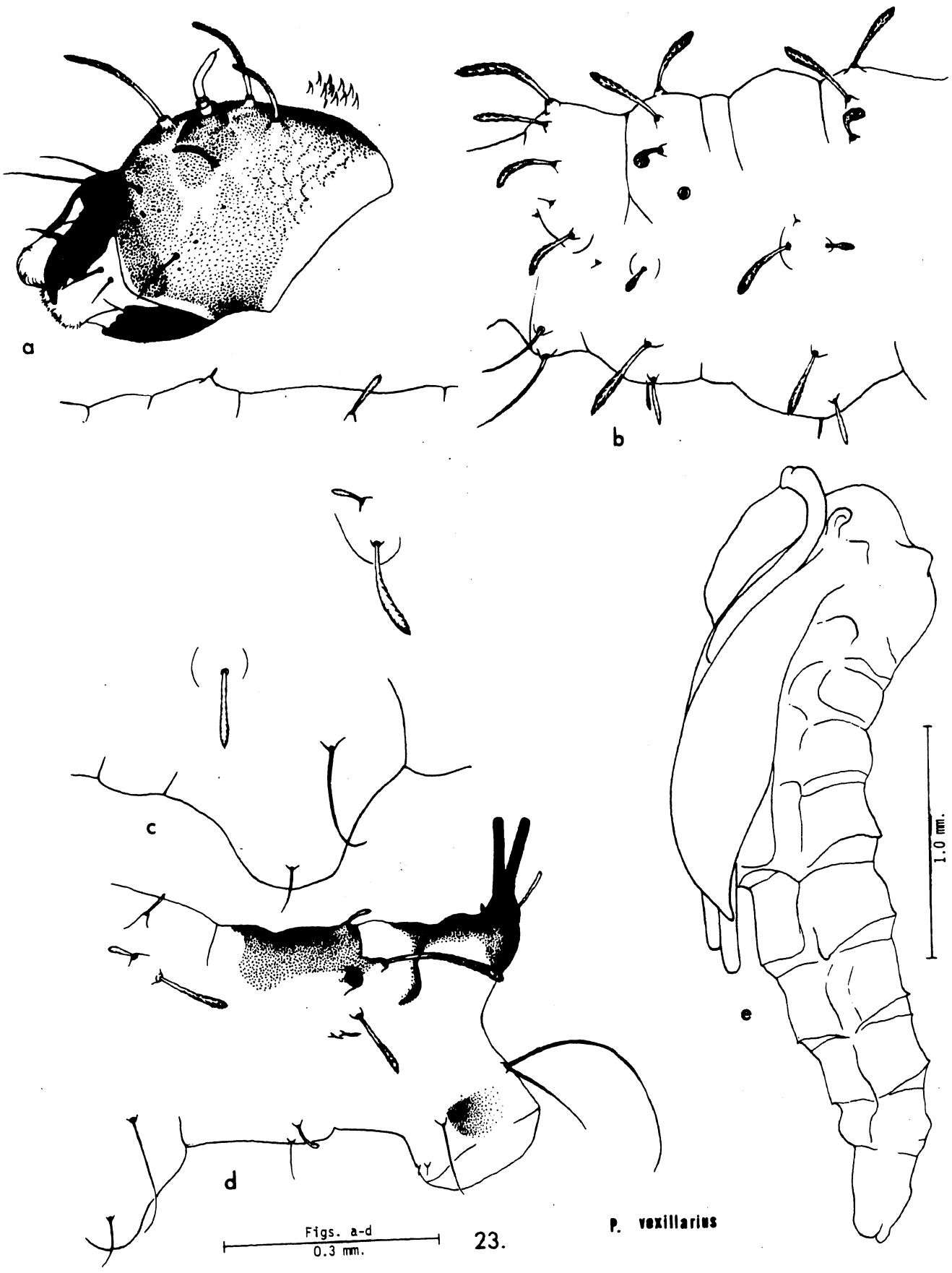

b
c
a
d
e
f
1.0 mm.
Figs. b-e
0.3 mm.
P. vespertilionis

PLATE 23

Phlebotomus vexillarius

Figures a - d. Fourth instar larva (a. Head, b. Prothorax and mesothorax, c. Third abdominal segment, d. Seventh and eighth abdominal segments.)

Figure e. Pupa.



23. P. vexillarius

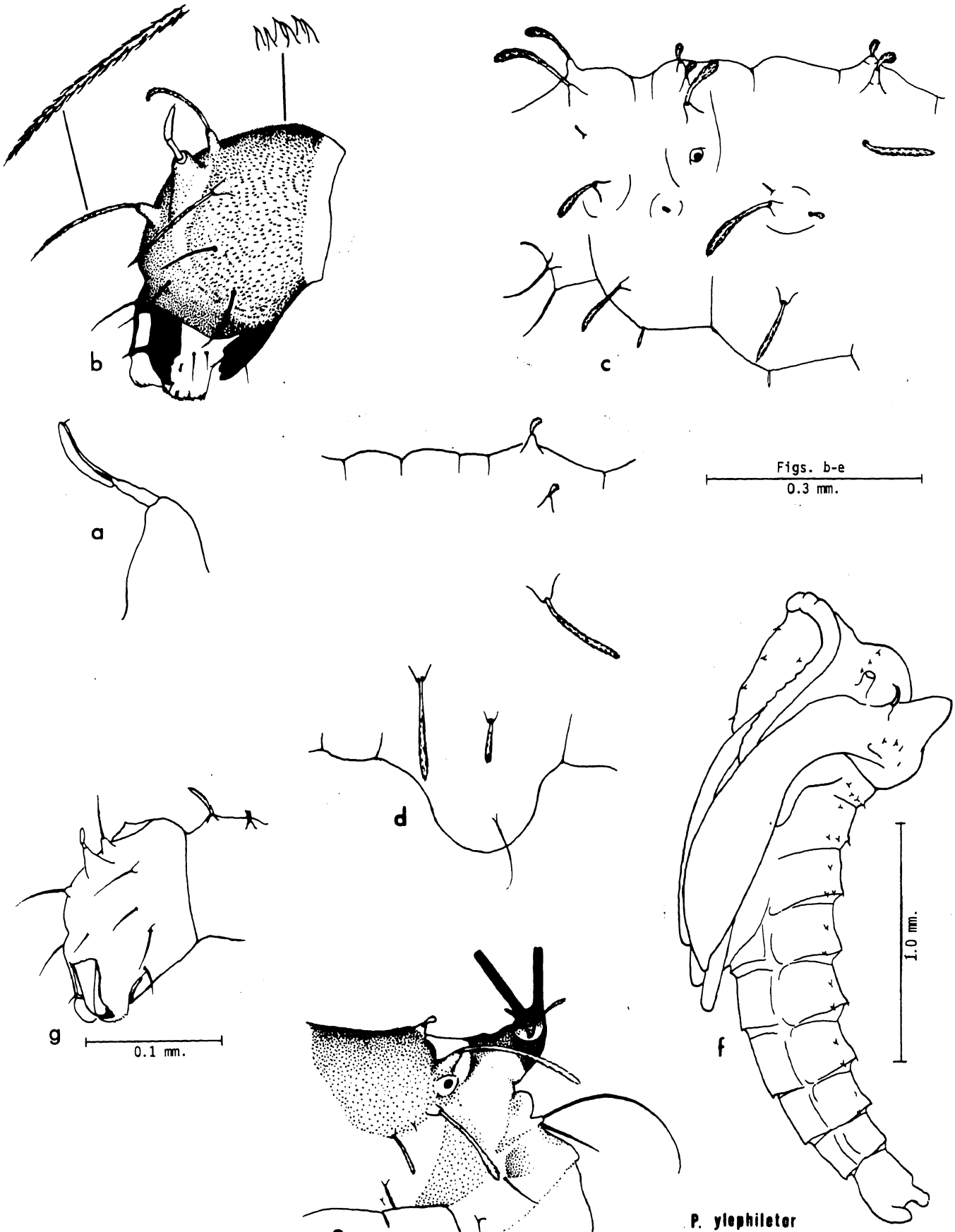
PLATE 24

Phlebotomus ylephiletor

Figures a - e. Fourth instar larva (a. Antenna, b. Head, c. Prothorax and mesothorax, d. Third abdominal segment, e. Eighth abdominal.)

Figure f. Pupa.

Figure g. Head of first instar larva.



P. ylephiletor

PLATE 25

Phlebotomus hansoni

Figures a - c. Exuvia of fourth instar larva (a. Antenna, b. Head and thoracic region, c. Seventh and Eighth abdominal segments.)

Figure d. Pupa

Phlebotomus carpenteri

Figure e. Head and prothorax of first instar larva.

Phlebotomus barrettoi

Figure f. Head of first instar larva.

Phlebotomus pinealis

Figure g. Head of first instar larva, laterodorsal aspect.

Phlebotomus dasymerus

Figure h. Head of first instar larva

Warileya rotundipennis

Figures i - k. First instar larva (i. Head, j. Antenna, k. Entire body.)

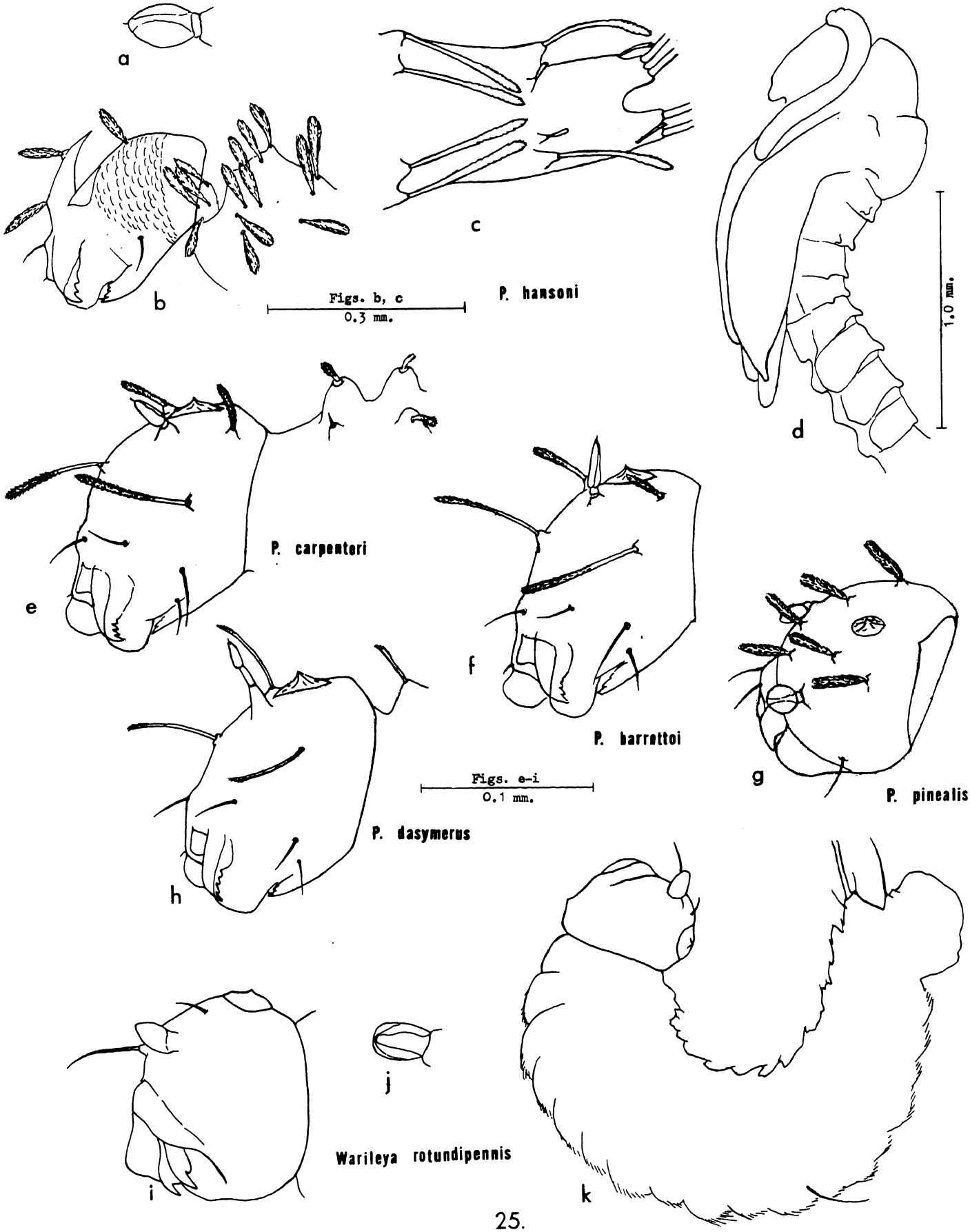
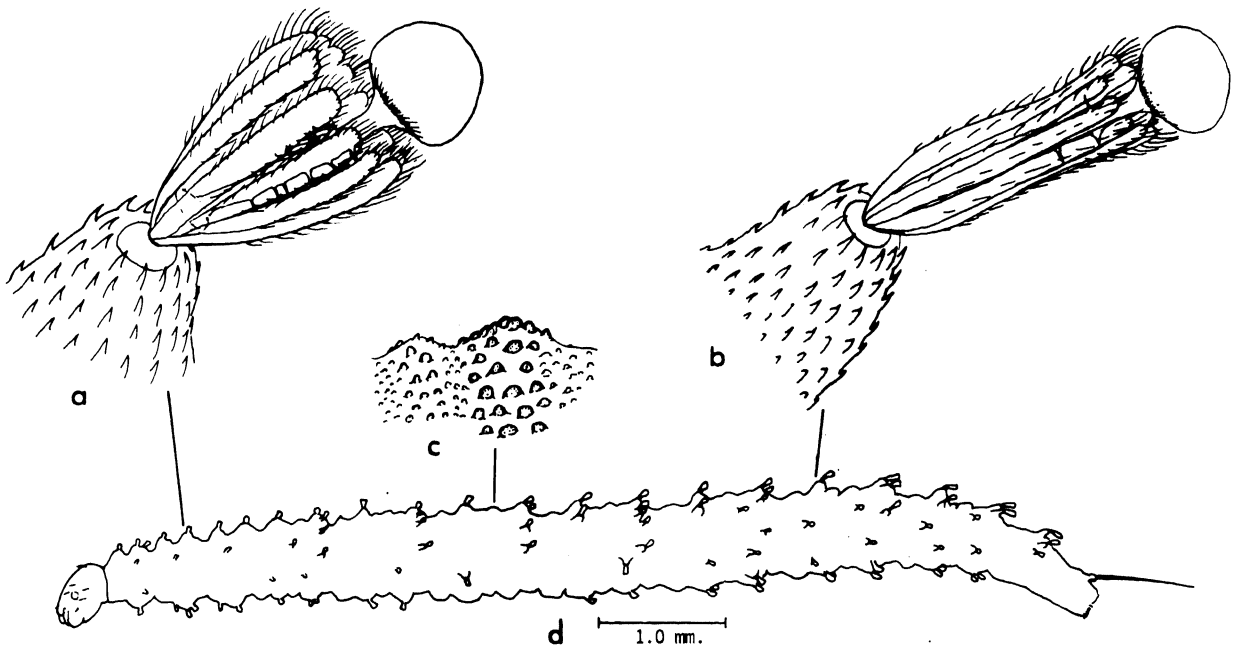

a
b
c
d
1.0 mm.
Figs. b, c
0.3 mm.
P. hansoni
P. carpenteri
e
f
P. barrettoi
g
P. pinealis
Figs. e-i
0.1 mm.
P. dasymerus
h
i
j
Warileya rotundipennis
k

PLATE 26

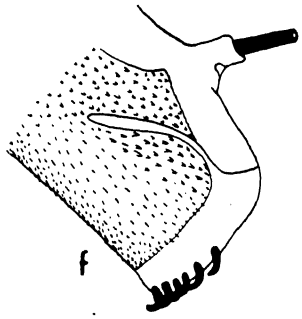
Nemopalpus sp.

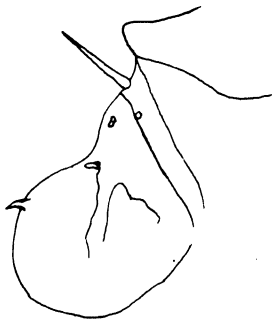
Figures a - j. Fourth instar larva (a. Dorsal brush-like seta of mesothorax, b. Dorsal brush-like seta of abdomen, c. Tubercles on integument, high magnification, d. Entire body, lateral aspect, f. Posterior end, g. Head, h. Mandible, i. Maxilla, external aspect, j. Maxilla, internal aspect.)

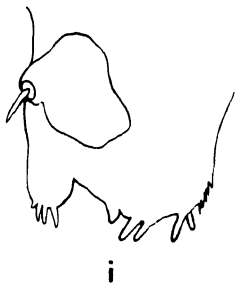
Figures k - l. First instar larva (k. Head and prothorax, l. Posterior segments.)

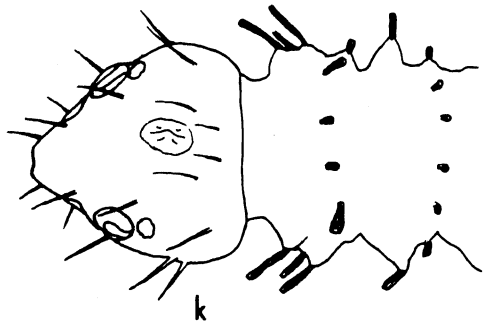


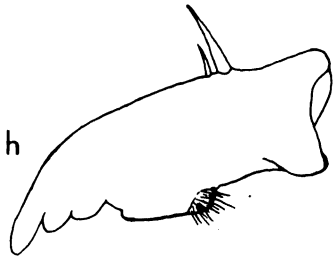
Nemopalpus sp.

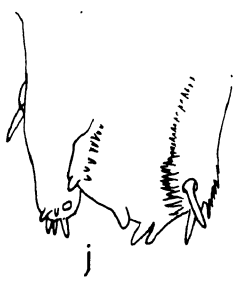












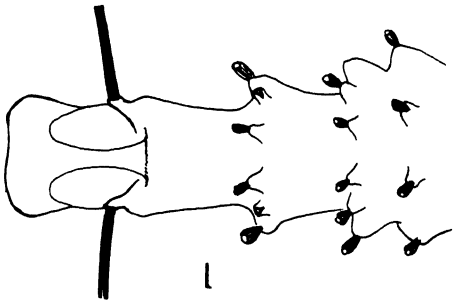


PLATE 27

A comparison of the larval classification with that of Fairchild (1955) based on adult characters.

CLASSIFICATION OF PHLEBOTOMINAE